



This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

### Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

- + *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.
- + *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.
- + *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.
- + *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

### About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at <http://books.google.com/>

JP

**Library  
of  
Arnold Arboretum**



of

**Harvard University**

E

K45.3

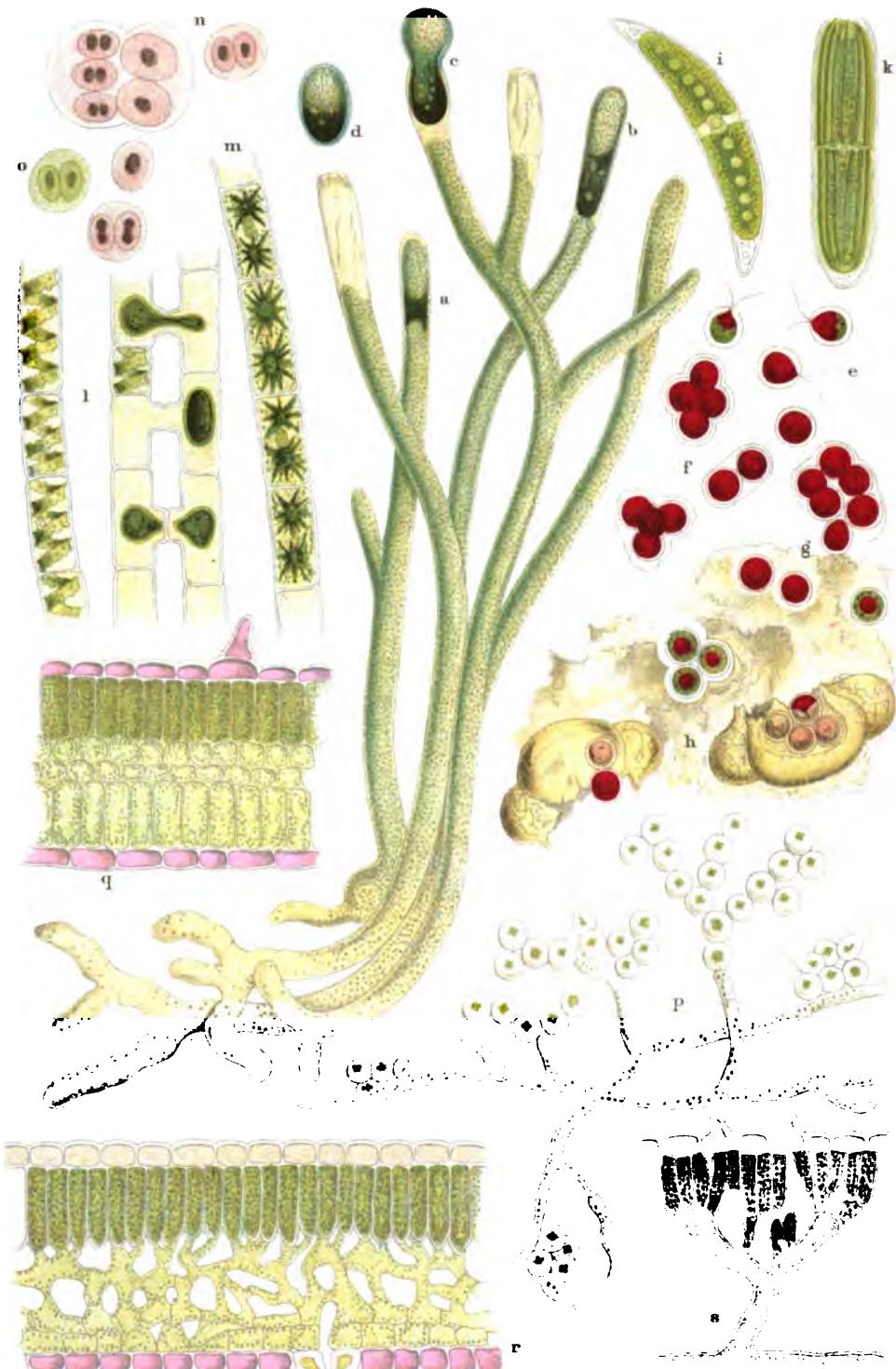
m







152



SWARM-SPORES AND ZYGOSPORES. FORMS OF  
CHLOROPHYLL-BODIES.

## SWARMSPORES AND ZYGOSPORES.

### FORMS OF CHLOROPHYLL-BODIES.

- a—d Development of swarmspores in the tubular cells of *Vaucheria clavata*.  
e—h Swarmspores and resting-cells of "red-snow" (*Sphaerella nivalis*), mixed with pollen-grains of Pines.  
i—k Forms of Chlorophyll in cells of Desmidiae (i. *Closterium Leibleinii*; k. *Penium interruptum*).  
l Formation of zygospores and spiral arrangement of Chlorophyll-bodies in cells of *Spirogyra arcta*.  
m Star-shaped Chlorophyll-bodies in cells of *Zygnema pectinatum*.  
n—o *Gloeocapsa sanguinea*.  
p Protonema of *Schistostega osmundacea*.  
q Transverse section of the foliage-leaf of Cress.  
r Transverse section of the leaf of the Passion-flower.  
s Relative positions of laticiferous tubes and palisade-cells in the leaf of a Spurge (*Euphorbia Myrsinifolia*).

All the figures greatly magnified.



THE  
NATURAL HISTORY OF PLANTS  
THEIR FORMS, GROWTH,  
REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF  
**ANTON KERNER VON MARILAUN**  
PROFESSOR OF BOTANY IN THE UNIVERSITY OF VIENNA

BY  
**F. W. OLIVER, M.A., D.Sc.**  
QUAIN PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON

WITH THE ASSISTANCE OF  
**MARIAN BUSK, B.Sc. AND MARY F. EWART, B.Sc.**

WITH ABOUT 1000 ORIGINAL WOODCUT ILLUSTRATIONS AND SIXTEEN PLATES IN COLOURS

HALF-VOLUME I.



NEW YORK  
HENRY HOLT AND COMPANY  
1895



THE  
NATURAL HISTORY OF PLANTS  
THEIR FORMS, GROWTH,  
REPRODUCTION, AND DISTRIBUTION

FROM THE GERMAN OF  
**ANTON KERNER VON MARILAUN**

PROFESSOR OF BOTANY IN THE UNIVERSITY OF VIENNA

BY

**F. W. OLIVER, M.A., D.Sc.**  
QUAIN PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON

WITH THE ASSISTANCE OF

MARIAN BUSK, B.Sc. AND MARY F. EWART, B.Sc.

WITH ABOUT 1000 ORIGINAL WOODCUT ILLUSTRATIONS AND SIXTEEN PLATES IN COLOURS

HALF-VOLUME I.



NEW YORK  
HENRY HOLT AND COMPANY  
1895







525  
11

knowledge, yet there is no doubt that, as in art, the effect was to stimulate and reform; and that this study led up to the source, so long forgotten, whence the ancients had themselves drawn their knowledge, that is, to the direct investigation of nature, which has invariably given to every branch of human knowledge new and pregnant life.

As regards botanical knowledge in particular, the study of old Greek writings on the part of western nations in both Northern and Southern Europe had the immediate effect of instituting an eager search for all the different kinds of indigenous plants; and, besides arousing a passion for investigation, it evoked untiring industry in this pursuit, the results of which preserved in a number of bulky herbals still excite our wonder and respect. If these folios, dating for the most part from the first half of the sixteenth century, are perused in the hope of their revealing some guiding principle as a basis for the arrangement of the subject, the reader will no doubt be obliged to lay them aside unsatisfied. The plants were described and discussed just as the authors happened to come across them; and it is only here and there that we find a feeble attempt to range together and make groups of nearly-allied species. Only cursory attention was paid to the facts of geographical distribution. Plants native to the soil, herbs which flowered in gardens and had been reared from seed purchased from itinerant vendors of antidotes, and plants whose fruits were brought to Europe as curiosities from the New World recently discovered—all these were jumbled together in a confused medley. The whole endeavour of the time was directed to the enumeration and description of all such things as possess the power of producing green foliage and maturing fruit under the sun's quickening rays.

Owing to the fact that researches were then limited to the native soil of the student, most of the botanical authors of that day had but dark inklings of the extent to which the floras of various latitudes and areas differ. They assumed that plants of the Mediterranean shores, which had been described centuries before by Theophrastus or Dioscorides or Pliny, were necessarily the same as those of their own more inclement countries. The German "Fathers of Botany" (Brunfels, born about 1495, died 1534; Bock, 1498–1554; Fuchs, 1501–1566, are the best known) applied the old Greek and Latin names without scruple to the species growing in their own localities. They were so firmly convinced of the identity of the German, Greek, and Italian floras that even the numerous inconsistencies occurring in the descriptions did not disconcert them, or prevent them from discussing at great length whether a particular name was intended by Theophrastus and Dioscorides to indicate this or that plant. It was by slow degrees that botanists first began to abandon these fruitless debates concerning the Greek and Latin names of plants, with which it had been the custom to fill so many pages of the herbals. Step by step they became conscious that although the yellow pages of the ancient books deserved all gratitude for the stimulating influence they had exercised, yet the green book of nature should be set above them. This led to their devoting themselves entirely to direct researches in the subject of their native floras. The

herbal of Hieronymus Bock, which appeared in 1546, and in which "the herbs growing in German countries are described from long and sure experience," contains a passage treating of the controversy of the day as to whether the Latin name *Erica* was applicable to the German Heath or not; and in the midst of the discussion the author expresses the opinion that "the plants we know best were the least known to the Latins;" and at last he exclaims: "Be our heath the same as *Erica* or not, it is in any case a pretty and sturdy little shrub, beset with numerous brown rounded branches, which are clothed all over with small green leaves; and its appearance is like that of the sweet-smelling Lavender Cotton." And again in a number of other places, after making lengthy philological statements relating to the old names, he ends by losing patience and declaring that the proper thing would be to lay aside all disputes concerning this nomenclature.

At length a Belgian, Charles de l'Ecluse (1526-1609), whose name was latinized into Clusius, emancipated himself entirely from the hair-splitting verbal controversies of the day. He was also the first to abandon the utilitarian standpoint; and in his extensive work, which appeared at the end of the sixteenth century, he was guided solely by the desire to become acquainted with every flowering thing. He therefore endeavoured to distinguish, describe, and where possible to draw the various forms of plants, to cultivate them, and to preserve them in a dried condition. It was just at that time that collections of dried plants began to be made. Such a collection was at first called a "hortus siccus," and later on a "herbarium." All museums of natural history were forthwith furnished with them. Moreover, Clusius, actuated by the wish to see with his own eyes what the vegetation on the other side of the mountains looked like, was the first man to travel for the purpose of botanizing. In order to extend his knowledge of plants he roamed over Europe from the sierras of Spain to the borders of Hungary, and from the sea-coast to the highlands of the Tyrol. Journeys of this kind in pursuit of botanical knowledge were by degrees extended to wider and wider limits, and thus an abundance of material was brought together from all latitudes and from every quarter of the globe.

An immense number of isolated observations were accumulated in this way, till, at length, in the first decades of the eighteenth century, the desirability of sifting and arranging this chaotic mass became urgent. When, therefore, the Swedish naturalist Linnæus (1707-1778), by the exercise of unparalleled industry, mastered in a fabulously short space of time the detailed results of centuries of labour, and afforded a general survey of all this scattered material, he obtained universal recognition. Linnæus introduced short names for the various species in place of the cumbrous older designations, and showed how to distinguish the species by means of concise descriptions. For this purpose he marked out the different parts of a plant as root, stem, leaf, bract, calyx, corolla, stamens, pistil, fruit, and seeds. Again, he distinguished particular forms of those organs, as, for instance, scapes, haulms, and peduncles as forms of stems, and in addition also the parts of each organ, such as filaments, anthers, and pollen in the stamens, and ovary, style, and stigma in the pistil; and to each one of these objects he assigned a technical name

(*terminus*). With the help of the botanical terminology thus formulated it became possible not only to abridge the specific descriptions, but also to recognize species from such descriptions, and to determine what name had been given them by botanists, and to what group they belonged.

Linnæus selected as a basis of classification in the "System" established by him the characteristics of the various parts of the flower. In this system the number, relative length, cohesion, and disposition of the stamens formed the ground of division into "Classes." Within each Class, "Orders" were then differentiated according to the nature of the pistil, especially the number of styles; and each Order was again subdivided into more narrowly defined groups, which received the name of "Genera." To the 23 classes of Flowering Plants (*phanerogamia*) Linnæus added as a 24th Class Flowerless Plants (*Cryptogamia*), which were divided into several groups (Ferns, Mosses, Algae, and Fungi) in respect of their general appearance and mode of occurrence.

This system took immediate possession of the civilized world. Englishmen, Germans, and Italians now worked in unison as faithful disciples of Linnæus. Even laymen studied the Linnæan botany with enthusiasm; and it was recommended, especially to ladies, as a harmless pastime, not overtaxing to the mind. In France Rousseau delivered lectures on botany to a circle of educated ladies; whilst even Goethe experienced a strong attraction to the "loveliest of the sciences," as botany was called in that day. Linnæus had introduced for the first time the name "flora" to signify a catalogue of the plants of a more or less circumscribed district. He had himself written a flora of Lapland and Sweden, and by doing so had stimulated others to undertake the compilation of similar catalogues; so that by the end of the 18th century floras of England, Piedmont, Carniola, Austria, &c., had been produced. By this means a certain perfection was attained in that field of botany which has only in view the examination of the fully-developed external forms of plants, together with the distinguishing, describing, naming, and grouping them, and the enumeration of species indigenous to particular regions. Later on, unfortunately, botanists lost themselves in a maze of dull systematizing. They either contented themselves with collecting, preparing, and arranging herbaria, or else devoted their energies to endless debates over such questions, for instance, as whether a plant, that some author had distinguished from others and described, deserved to rank as a species, or should be reckoned as a variety dependent on its habitat or on local conditions of temperature, light, and moisture. They took delight in now including a group of forms as varieties of a single species, now dividing some species as described by a particular author into several other species. For this purpose they did not rely upon the only sure method, the determination by cultural experiment of the fact of the constancy or variability of the form in question; nor did they, in general, adhere to any consistent principle to guide them in this amusement.

Aberrations of this kind constituted, however, no serious barrier to progress. On the contrary, the passion for collecting continued to extend its range. The

vegetation of the remotest corners of the earth was ransacked by travelling botanists without any material advantage being gained, though they not infrequently ran considerable risk to their health, and sometimes sacrificed their lives. As one generation succeeded another thousands of students of the "scientia amabilis" made their appearance in every country. Swept along by the prevailing current of thought they devoted themselves to the examination of native and foreign floras, or to a detailed study of the most insignificant sections of the vegetable kingdom. Those who are not under the spell of this passion cannot conceive the joy experienced by the discoverer of a hitherto unknown moss. To such it is inexplicable how anyone can devote the labour of half a lifetime to a classification of *Algæ* or Lichens, or to a monograph of the bramble-tribe or orchids. The progress achieved eventually in this department of botany is best appreciated when the wide difference in the numbers of species described in botanical works of different periods is considered. Theophrastus in his *Natural History of Plants* (about 300 B.C.) mentions about 500 species, and Pliny (78 A.D.) rather more than 1000; whereas, by the time of Linnæus, about 10,000 were known; and now the number must be all but 200,000. It should be remarked, however, that half the plants described since Linnæus lived fall into the category of Cryptogams, or non-flowering plants, the examination of which was first rendered possible by the widespread use of the microscope in recent times.

The microscope led also to discoveries concerning the internal architecture of plants. A faint attempt in this direction, made 200 years ago, had died away without leaving any trace behind; but at the commencement of this century the "*inward construction* of plants" was studied all the more eagerly by means of the microscope. In buildings belonging to different styles of architecture it is not only the forms of the wings, stories, rooms, and gables that differ, but also and in no less degree those of the columns, pilasters, and decorations. The same is the case with plants. They possess chambers at different levels, vaults, and passages. They have pipes running through them, and beams and buttresses, some massive and some slender, to support them. The pieces of which they are built vary in size, and their walls are sculptured in all kinds of ways. It was the business of the vegetable anatomist to dissect plants, to look into all these structures under the microscope, to describe the various component parts as well as the ground-plan and elevation of the plant-edifice as a whole; and to name the different forms of structure after the manner of Linnæus when he invented terms for the different forms of stems and leaves, and for the several parts of the flower and fruit.

#### DOCTRINE OF METAMORPHOSIS AND SPECULATIONS OF NATURE-PHILOSOPHY.

Side by side with this immense volume of research, which was directed to the separation, description, and synoptical arrangement of mature forms only, there arose about the year 1600 another school which considered vegetable forms from

the point of view of their life-history, and endeavoured to trace them back to their origin. Tracing the development, from one stage to another, of all the different species, of the multitudinous forms of leaves and flowers, and of the various kinds of cells and tissues, the student of this school has to detect identity in multiplicity, to show that the connection between forms which have arisen from one another is in accordance with fixed laws, and to express those laws in definite formulae.

The attention of botanists was in the first place directed to the wonderful series of changes in the form of the leaf which occur in all phanerogamic (*i.e.* flowering) plants as the delicate seedling gradually turns into a flowering shoot. At the circumference of the stem which constitutes the axis of the plant, foliar structures are produced at successive intervals. All these structures are essentially the same; but they exhibit a continuous modification of their shape, arrangement, size, and colour, according to their relative altitudes upon the stem. To discover the causes of this structural variation was an attractive problem, and very diverse theories were suggested for its solution. The earliest explanation, which was given by the Italian botanist Cesalpino in 1583, is founded rather on superficial analogies and remote resemblances existing between tissues than on careful observation. According to this theory the stem is composed of a central medulla highly endowed with vitality, and surrounded by concentric layers of tissue, those namely of the wood, the bast, and the cortex. Each of the foliar structures put forth from the axis is supposed to originate in one of the above-named tissues, the idea being that the green foliage-leaf and calyx grew out from the cortical layer, the corolla from the bast, the stamens from the wood, and the carpels from the medulla. It was believed, also, that the outer envelope of a fruit arose from the rind of the fruit-stalk, the seed-coats from the wood, and the central part of the seed from the medulla.

Early in the eighteenth century there came to be connected with this theory the doctrine of so-called "prolepsis," which was founded on more accurate comparative observations. It was thought that the medulla of the stem breaks through the rind at particular spots to form at each a bud, which subsequently grows out into a side branch. Owing to this lateral pressure of the medulla the ascending nutrient sap becomes arrested beneath the rudimentary bud, and, in consequence, the cortex develops under the bud into a foliage-leaf. In the bud the different parts of the future annual shoot are already shadowed forth in stages one above the other; and each is produced always by the one beneath it. As soon as vegetative activity is resumed after the expiration of the winter rest, the bud sprouts. If only that part of it develops which constitutes the first year's rudiment, a shoot furnished with foliage-leaves is produced. But the embryonic structures belonging to succeeding years, which are concealed in the bud, may also be stimulated to development; and when this happens, these premature products do not appear as foliage-leaves, but in more or less altered forms as bracts, sepals, petals, stamens, and carpels. If no such anticipatory activity has been excited, the rudiment which in the previous case would have developed into a bract does not appear till the following year, and then as a foliage-leaf; whilst that which would have formed a calyx in the first

year lies dormant till the third year, when it too emerges simply as a leaf. This transformation of the leaves, or metamorphosis as Linnæus called it, is, therefore, the result of anticipation; and it was assumed by the Linnæan school that the cause of this metamorphosis or hastened development was a local decrease in the quantity of nutriment. The idea was, that in consequence of the limited supply of sap the incipient leaves were not able to attain to the size of foliage-leaves, but remained



Fig. 1.—Seedlings with Cotyledons and Foliage-leaves.

<sup>1</sup> *Cytisus Laburnum*. <sup>2</sup> *Koelreuteria paniculata*. <sup>3</sup> *Acer platanoides*.

rudimentary, as is the case with many bracts; and further, that the axis was no longer capable of elongating, so that the leaves proceeding from it remained close together, became coherent, and thus formed the calyx. The supporters of this explanation relied particularly on the experience of gardeners, that a plant in good soil with a liberal supply of nutriment is apt to produce leafy shoots rather than flowers; whereas, if the same plant is transferred to a poorer soil, where its food is limited, it develops flowers in abundance.

But yet a third attempt was made to explain this process of transformation, by the theory that parts which are identical so far as their origin is concerned, subsequently receive the stamp of distinct foliar organs. The diversity in the development of parts, originally alike, was supposed to depend on a filtration of the nutrient

sap, the idea being that identical primordial leaves issuing from the axis of a particular plant were fashioned with more and more delicacy as the sap became clarified and refined in its passage through the vessels. This explanation of metamorphosis was first given by Goethe (1790) in a treatise which was much discussed, and which exercised a most important influence in initiating researches of a similar nature. Goethe's interpretation of metamorphosis may be briefly reproduced as follows. A plant is built up gradually from a fundamental organ—the leaf—which issues from the node of a stem. First of all, the organs which are called seed-leaves or cotyledons (fig. 1) develop on the young plant as it germinates from the seed; they proceed from the lowest node of the stem, and are frequently subterranean. They are of comparatively small size, are simple and unsegmented, have no trace of indentation, and appear for the most part as thick, whitish lobes, which are, according to Goethe's expression, closely and uniformly packed with a raw material, and are only coarsely organized. Goethe explains these leaves as being of the lowest grade in the evolutionary scale. After them and above them the foliage leaves develop at the succeeding nodes of the stem; they are more expanded both in length and breadth; their margins are often notched, and their surfaces divided into lobes, or even composed of secondary leaflets; and they are coloured green. "They have attained to a higher degree of development and refinement, for which they are indebted to the light and air." Still further up, there next appears the third stage in foliar evolution. The structure called by Linnæus the calyx is again to be traced back to the leaf. It is a collection of individual organs of the same fundamental type, but modified in a characteristic manner. The close-set leaves, which proceed from nodes of the stem at what is, in a certain sense, the third story of the plant-edifice as a whole, and which constitute the calyx, are contracted, and have but little variety as compared with the outspread foliage-leaves.

On the fourth rung of the ladder by which the leaf ascends in its effort to perfect itself, appears the structure named in the Linnæan terminology the corolla. It consists, like the calyx, only of several leaves grouped round a centre. If a contraction has taken place in the case of the calyx, we have now once more an expansion. The leaves which compose the corolla are usually larger than those of the calyx. They are, besides, more delicate and tender, and are brightly coloured; and Goethe, whose mode of expression is here preserved as far as possible, supposes them to be filled also with purer and more subtle juices. He conceives that these juices are in some manner filtered in the lower leaves and in the vessels of the lower region of the stem, and so reach the upper stories in a more perfect condition. A more refined sap must then, he says, give rise to a softer and more delicate tissue (fig. 2). Above the corolla and at the fifth stage of development there follows the group of stamens, structures which, though not answering to the ordinary conception of leaves, are yet to be regarded again simply as such. In the circle of the corolla the leaves were expanded, and conspicuous owing to their colour; on the other hand, in the stamens they are contracted to an extreme degree, being almost filamentous in part. These leaves appear to have reached a high degree of perfection,

and in the parts of the stamens termed anthers "pollen-grains" are developed "in which an extremely pure sap is stored." Adjoining these pollen-producing leaves,



Fig. 2.—Metamorphoses of Leaves as exhibited by the Poppy.

<sup>1</sup> Germinating plant with cotyledons. <sup>2</sup> and <sup>3</sup> The same plant further developed and with foliage-leaves; in <sup>2</sup> the cotyledons and lowest foliage-leaves are already withered. <sup>4</sup> The same plant with a flower-bud showing the closed sepals. <sup>5</sup> The bud open and with petals, stamens, and carpels (pistil) developed.

where contraction has reached its extreme limit, is the sixth and last story, which is composed of leaves, once more less closely-set, and exhibiting a final expansion on the part of the plant. These are the carpels, which surround the highest part

of the stem and inclose the seeds, the latter being developed from the tip of the stem. Thus the plant accomplishes its life-history in six stages. It is built up of leaves, the "intrinsic identity" of which cannot be doubted, although they assume extremely various shapes corresponding to the six strides towards perfection. In this process of transformation or metamorphosis of the leaf there are three alternate contractions and expansions, whilst each stage is more perfect than the one next below it.



Fig. 2.—Goethe's "Urpflanze."

Whilst seeking to explain metamorphosis in this manner, and endeavouring, with greater perspicacity than all his predecessors and contemporaries, "to reduce to one simple universal principle all the multifarious phenomena of the glorious garden of the world," Goethe conceived the notion of a typical plant, an ideal, the realization of which is achieved in nature by means of a manifold variation of individual parts. This abstract notion of a plant's development with its six stages corresponding to "three wave-crests" or expansions (Leaf, Petal, Carpel) and "three wave-troughs" or contractions (Cotyledon, Sepal, Stamen) is expressed graphically in figure 3. It still holds its ground at the present day under the name of Goethe's "Urpflanze," and the credit of its invention is entirely his. But it is not quite right to claim for Goethe, in addition, the title of founder of the doctrine of vegetable metamorphosis; for in reality he only offered another interpretation and mode of representation of a phenomenon already included by Linnæus under the term *metamorphosis*. Linnæus had instituted a

comparison between the metamorphosis of plants and that of insects; in particular, he likened the calyx to the ruptured integument of a chrysalis and the internal parts of a flower to the perfect insect (*Imago*). He also made many different attempts to establish analogies between the development of plants and that of animals; and in so doing he opened up a wide field for the speculations of the "nature philosophers" in the earlier part of the nineteenth century.

An extensive study of this subject now commenced; and writers on nature-philosophy worked indefatigably at the amplification and modification of this theme, first broached by Linnæus.

"A plant is a magnetic needle attracted towards the light from the earth into the air. It is a galvanic bubble, and, as such, is earth, water, and air. The plant-bubble possesses two opposite extremities, a single terrestrial end and a dual aërial end; and so plants must be looked upon as being organisms which manifest a

continual struggle to become earth on the one hand and air on the other, unmixed metal at one end, and dual air at the other. A plant is a radius, which becomes single towards the centre, whilst it divides or unfolds towards the periphery; it is not therefore an entire circle or sphere, but only a segment of one of those figures. The individual animal, on the contrary, constitutes of itself a sphere, and is therefore equivalent to all plants put together. Animals are entire worlds, satellites or moons, which circle independently round the earth; whereas plants are only equal to a heavenly body in their totality. An animal is an infinitude of plants. A blossom which, when severed from the stem, preserves by its own movement the galvanic process or life, is an animal. An animal is a flower-bubble set free from the earth and living alone in air and water by virtue of its own motion."

Page after page of the writings on *Nature-philosophy* of Oken (1810) and other contemporary naturalists is filled with interminable statements of the same kind. At the present day it seems scarcely credible that such propositions were then received with admiration as profound and ingenious utterances, and that they were even adopted as mottoes for botanical and geological treatises. For example, it is worthy of record that as late as the year 1843 the Austrian botanist Unger made use of the last of the flowers of rhetoric above quoted from Oken's *Nature-philosophy* as a motto for one of his first works on the history of development, the title of which is *Plants at the Moment of their becoming Animals*.

The general divisions or systems of the vegetable kingdom which were evolved by adherents of the school of Nature-philosophy were, as may be imagined, just as absurd as the speculations on which they were based. In his *Philosophical Systems of Plants* Oken develops in the first place the idea that the vegetable kingdom is a single plant taken to pieces. Inasmuch as the ideal highest plant is composed of five organs, there must likewise be five classes: root-plants, stem-plants, leaf-plants, flower-plants, and fruit-plants. The world is fashioned out of the elements: earth, water, air, and fire. Hereupon is founded a classification of root-plants into earth-plants or lichens, water-plants or fungi, air-plants or mosses, and light-plants or ferns. Proceeding from the assumption that all the groups are parallel and that the principle of classification for each group is always given by the one preceding it, we have next, to take one instance, the second class—that of stem-plants—divided (in accordance with the subdivision of earth into earths, salts, bronzes, and ores) into earth-plants or grasses, salt-plants or lilies, bronze-plants or spices, and ore-plants or palms.

#### SCIENTIFIC METHOD BASED ON THE HISTORY OF DEVELOPMENT.

Though as we see the doctrine of metamorphosis, with its conception of a typical plant, degenerated thus into the most barren of fancies, still from it originated the line of research based on the history of development which has since borne fruit in every department of botany. Observers arrived at the conviction that every living plant undergoes a continuous transformation which follows a definite

course, and that accordingly every species is constructed on a plan fixed within general limits and exhibiting variation in externals only. These, it is true, are often more conspicuous at first sight than the direction and disposition of the parts which are really fundamental, and secure the stability of the entire structure. But in order to ascertain the plan of construction it was found necessary to go back to the very first visible appearance of each organ; to determine how the original rudiments of the embryo and the beginnings of roots, stems, leaves, and parts of the flower are formed, and to see what rudiments succeed in opening out, branching and dividing, and what remain behind to perish and be displaced by organs growing vigorously in close proximity to them.

These researches into the course of development of the separate parts of flowering plants, and to a still greater extent the observations of the development of cryptogams or spore-plants (rendered possible by improvements in the construction of microscopes), led naturally to a study of the history of the elementary structures of which all plants are composed. Previously three kinds of elementary organs had been supposed to exist, utricles, vessels, and fibres. The observations of Brown and Mohl (1830-1840) resulted, however, in the identification of the cell as the common starting-point of all these elementary organs. This led to the further discoveries that protoplasm is the formative and living part of a cell, and that each cell is differentiated into a protoplasmic cell-body and a cell-membrane. It followed that the envelope of the protoplasmic body, the cell-membrane, which had hitherto been considered the primary formation, was in reality a *product* of the protoplasm enveloped by it, and this discovery resulted in a complete revolution in the conception of cells generally. Further investigation led to the conclusion that the various modes of growth and multiplication depend on definite laws. That even in the mode of juxtaposition of daughter-cells arising in reproduction, a certain plan of construction may be distinguished in each species which must stand ultimately in some causal relation to the structural system of the whole plant. The progress achieved along these lines in the course of a few decades has been extraordinarily great, no doubt due to the peculiar fascination which the study of the life-histories and transformations of living organisms and the observation of mysterious processes invisible to the naked eye have had for the mind of the inquirer.

In that group of plants which includes the forms classed together by the earlier botanists under the name of Cryptogamia an altogether new world was revealed. An undreamed-of variety was discovered to exist in the processes of propagation and rejuvenescence of these forms of plants by means of single cells or spores. Objects which, having regard to their external form, had been assigned to widely different groups, were found to be connected with one another as stages in the development of one and the same species; and one result of these discoveries was the establishment in this division of the vegetable kingdom of an entirely new system of classification based on life-histories. The systematic arrangement of Flowering-plants or Phanerogams also underwent essential alteration. The Linnaean system, founded on the numerical relations between the different parts of the flower,

had indeed already been displaced by another method of classification, that of the French observers Jussieu (1789) and De Candolle (1813), who framed systems said to be natural when contrasted with the artificial system of Linnæus. At bottom, however, these classifications only differed from the Linnæan in the fact that they multiplied and widened the grounds of division. The main division of Phanerogamia into those which put forth one cotyledon (or seed-leaf) on germinating (*Monocotyledones*) and those whose seedlings bear two cotyledons (*Dicotyledones*) is the only one that could serve as a starting-point for a system based on the history of development; but when we come to the grouping of *Dicotyledones* into those destitute of corolla (*Apetalæ*), those with the corolla composed of coherent petals (*Monopetalæ*), and those with the corolla composed of distinct petals (*Dialypetalæ*), we have already to admit something forced, and a reliance on characteristics merely external.

The system which is the outcome of the study of development starts with the idea that similarity between adult forms is not always decisive evidence of their belonging to the same group, and that the relationships of different plants is much more surely indicated by the fact of their exhibiting the same laws of growth and the same phenomena of reproduction. Plants exhibiting widely different external forms in the mature state are nevertheless to be looked upon as closely allied if they are constructed according to the same plan, and *vice versa*. There can be no question that a system based on these principles means a material advance. At the same time it cannot be overlooked that great difficulties are involved in hitting upon the right selection from among the number of phenomena observed in the course of a plant's development, and in determining which of these phenomena are to be referred to a mode of construction common to a number of plants, and therefore treated as fundamental properties, and which should be esteemed merely as outcomes of the conditions of life affecting the existence of the plant in question.

#### OBJECTS OF BOTANICAL RESEARCH AT THE PRESENT DAY.

DESCRIPTIVE BOTANY only concerns itself with the configuration of a plant. COMPARATIVE MORPHOLOGY endeavours to trace back to a single prototype the extremely various forms exhibited by mature plants. The history of development deals with the growth and differentiation of such forms. But all these paths of research shirk the problem of the biological significance of the different forms. The line of investigation starting from the conception of a plant's life as a series of physical and chemical processes, and which attempts to elucidate the configuration of a plant in the light of its environment, could not be developed with the slightest prospect of success until physics, chemistry, and other allied sciences had reached a high degree of perfection, and till botanists had become convinced that the phenomena of life are only to be fathomed by means of experiment.

The earliest attempts to define the biological significance of the several parts of

a plant do, it is true, take one back as far as Aristotle and his school; but the ideas of vegetable life entertained at that time are scarcely more than fantastic dreams; and the recognition now accorded to them springs rather from a reverence for antiquity than from any intrinsic merit which they possessed. The first experimental investigations into the vital phenomena of plants were published by Stephen Hales in 1718; but it was not till a hundred years later that this kind of research really came into vogue. It brought with it the conception of a cell as a miniature chemical laboratory, and looked for mechanical interpretations of the phenomena of nutrition, sap-circulation, growth, movement—in short, all vital processes—and for some connection between these processes and the external form. Whereas, in the case of descriptive and speculative botany, and in the study of development, the entire plant was first taken into consideration, next its several parts, and lastly the cells and protoplasm; in the new department of inquiry, on the contrary, the complete histories of the ultimate organs were studied first of all, then the significance of the different forms of the several members, and lastly the phenomena occasioned by the aggregate life of all the various kinds of animals and plants.

Modern science, governed as it is by the desire to lay bare the causes of all phenomena, is no longer satisfied with knowledge concerning the existence of cells, the arrangement of the different forms of cell, the development of their contents, and the changes undergone by cell-membranes. At the present day we inquire what are the functions of the various bodies which are formed within the protoplasm? Why is the cell-membrane thickened at a particular spot in a particular manner? What is the meaning of all the tubes and passages which exhibit such great diversity of size and shape? What part is played by the peculiar mouths of these channels, and why do they vary so greatly in shape and distribution in plants which are subject to different external conditions? We are no longer content to determine in what manner the rudimentary organ of a plant is produced, or how it expands in one case and frequently divides, or else is arrested in its growth and shrivels up; but we inquire the reason why one rudiment grows and develops whilst another is obliterated. For us no fact is without significance. Our curiosity extends to the shape, size, and direction of the roots; to the configuration, venation, and insertion of the leaves; to the structure and colour of the flowers; and to the form of the fruit and seeds; and we assume that even each thorn, prickle, or hair has a definite function to fulfil. But efforts are also made to explain the mutual relations of the different organs of a plant, and the relations between different species of plants which grow together. Lastly, this department of research (the rapid growth of which is due to Darwin) includes amongst its objects a solution of the problem of the ultimate grounds of morphological variety, the causes of which can only be sought for in a qualitative variation of protoplasm. Specific relationship is explained by attributing it to similarity in the constitution of the protoplasm of allied species, and the affinities exhibited by living and extinct plants are used as means of unfolding the hereditary connection between the

thousands of different sorts of forms, and of tracing the history of plants and vegetable life all over the earth.

The various lines of botanical research described in the foregoing pages, with their particular problems and objects, have but slight connection one with another. They run side by side along separate paths, and it is only occasionally that a junction is apparent which establishes a communication between one path and another. The subject-matter, however, is always the same. Whether we have to do with the perfected form or with its growth, whether we try to interpret the processes of life or to trace the genealogy of the vegetable kingdom, we always start from the forms of plants; and the ultimate result is never anything more than a description of the varying impressions which we receive at different times from the objects observed, and which we endeavour to bring into mutual connection. All the different departments of botany are accordingly more or less limited to description; and even when we endeavour to resolve vital phenomena into mechanical processes we can only describe, and not really explain, what happens. The processes which we call life are movements. But the causes of those movements, so-called forces, are purely subjective ideas, and do not involve the conception of any actual fact, so that our passion for causality is only ostensibly gratified by the help of mechanics. Du Bois Reymond is not far wrong when he follows out this train of thought to the conclusion (however paradoxical it may sound) that there is no essential difference between describing the trajectory (or particular kind of curve) in which a projectile moves on the one hand, and describing a beetle or the leaf of a tree on the other.

But even though the ultimate sources of vital phenomena remain unrevealed, the desire to represent all processes as effects, and to demonstrate the causes of such effects—a desire which is at the very root of modern research—finds at least partial gratification in tracing a phenomenon back to its proximate cause. In the mere act of linking ascertained facts together, and in the creation of ideas involving interdependence among the phenomena observed, there lies an irresistible charm which is a continual stimulus to fresh investigations. Even though we be sure that we shall never be able to fathom the truth completely, we shall still go on seeking to approach it. The more imaginative an investigator the more keenly is he goaded to discovery by this craving for an explanation of things and for a solution of the mute riddle which is presented to us by the forms of plants. It is impossible to overrate the value and efficiency of the transcendent gift of imagination when applied to questions of Natural History. Thus when we inquire whether certain characters noted in a plant are hereditary, constant, and inalienable, or are only occasioned by local influences of climate or soil, and hence deduce whether the plant in question is to be looked upon as a species or a variety; when we conclude from the fact of a resemblance between the histories of the development of various species that they are related, and place them together in groups and series; when we unravel the genealogies of different plants by comparing forms still living with others that are extinct; when we try to represent clearly

the molecular structure of the cell-membrane by arguing from the phenomena manifested by that membrane; when we investigate the meaning of the peculiar thickenings and sculpturings of the walls of cells, or when we discover the strange forms of flowers and fruits to be mechanical contrivances adapted to the forms of certain animals, and judge the extent to which these contrivances are advantageous, or the reverse, to the plants—in all these and similar investigations imagination plays a predominant part. Experiment itself is really a result of the exercise of that faculty. Every experiment is a question addressed to nature. But each interrogation must be preceded by a conjecture as to the probable state of the case; and the object of the experiment is to decide which of the preliminary hypotheses is the right one, or at least which of them approaches nearest to the true solution. The fact that when the imagination has been allowed to soar unrestrained, or without the steady ballast of actual observations, it has frequently led its followers into error, does not detract at all from its extreme value as an aid to research, notwithstanding the fact that it is responsible for the wonderful fantasies of nature-philosophy of which a few specimens have been given. Nor should we esteem it the less because enlargements of the field of observation and improvements in the instruments employed have again and again led to the substitution of new ideas for those which careful observers and experimentalists had arrived at by collating the facts ascertained through their labours.

For the same reasons it is unfair to regard with contempt the ideas of plant-life formed by our predecessors. It should never be forgotten how much smaller was the number of observations upon which botanists had to rely in former times, and how much less perfect were their instruments of research. Every one of our theories has its history. In the first place a few puzzling facts are observed, and gradually others come to be associated with them. A general survey of the phenomena in question suggests the existence of a definite uniformity underlying them; and attempts are made to grasp the nature of such uniformity and to define it in words. Whilst the question thus raised is in suspense, botanists strive with more or less success to answer it, until a master mind appears. He collates the observed facts, gathers from them the law of their harmony, generalizes it, and announces the solution of the enigma. But observations continue to multiply; scientific instruments become more delicate, and some of the newly-observed facts will not adapt themselves to the scheme of the earlier generalization. At first they are held to be exceptions to the rule. By degrees, however, these exceptions accumulate; the law has lost its universality and must undergo expansion, or else it has become quite obsolete and must be replaced by another. So it has been in all past times, and so will it be in the future. Only a narrow mind is capable of claiming infallibility and permanence for the ideas which the present age lays down as laws of nature.

These remarks on the limitations of our knowledge of nature, the importance of imagination as an aid in research, and the variability of our theories are made with a view to moderate, on the one hand, the exuberant hopes raised by the belief

that the great questions connected with the phenomenon of life will be solved, and to correct, on the other, the habit of not appreciating impartially the various methods which have been and are still employed by different botanists. In our own time, adhering as we do to the principle of the division of labour, it has become almost universal for each investigator to advance only along a single, very narrow path. But owing to the fact that one-sidedness too often leads to self-conceit, the lines of study followed by others are not infrequently despised, just as overweening confidence in the infallibility of the discoveries of the present day leads to depreciation of the labours of former times.

For the building-up of the science of the Biology of Plants everything relating to the subject has its value, and is capable of being turned to account. Whether the materials are rough or elaborated, massive, fragmentary, or merely connective, howsoever and whensover they have been acquired, they all are useful. The study of dried plants made by a student in a provincial museum, the discoveries of an amateur regarding the flora of a sequestered valley, the contributions of horticulturalists on subjects of experiment, the facts gleaned by farmers and foresters in fields and woods, the disclosures which have been wrested from living plants in university laboratories, and the observations conducted in the greatest and best of all laboratories—that of Nature herself—all these results should be turned to account. Let us take for the motto of the following pages the text:

"Prove all things; hold fast that which is good."



# THE LIVING PRINCIPLE IN PLANTS.

---

## 1. PROTOPLASTS CONSIDERED AS THE SEAT OF LIFE.

*Discovery of the Cell.—Discovery of Protoplasm.*

### DISCOVERY OF THE CELL.

What is life? This ever-interesting question has seemed to approach nearer solution on the occasion of every great scientific discovery. But never did the hope of being able to penetrate the great secret of life appear better founded than at the time when, among other memorable developments of science, it was discovered that objects could be rendered visible on an enlarged scale by the use of glass lenses, and the microscope was invented. These magnifying glasses were expected to yield, not only an insight into the minute structure of living beings which is invisible to the naked eye, but also revelations concerning the processes which constitute life in plants and animals. The first discoveries made with the microscope, between 1665 and 1700, produced a profound impression on the observers. The Dutch philosopher Swammerdam became almost insane at the marvels revealed by his lenses, and at last destroyed his notes, having come to the conclusion that it was sacrilege to unveil, and thereby profane, what was designed by the Creator to remain hidden from human ken. The observations of Leeuwenhoek (1632-1723) with magnifying glasses formed by melting fine glass threads in a lamp, were for a long time held to be delusions; and it was not till the English observer Robert Hooke had confirmed the fact of the existence of the minute organisms seen by Leeuwenhoek in infusions of pepper, and had exhibited them under his microscope in 1667 at a meeting of the Royal Society in London, that doubts as to their actual existence disappeared. Indeed a special document was then drawn up and signed by all those who were satisfied, on the evidence of their own eyesight, of the accuracy of the observation; and this clearly shows how greatly people were impressed with the importance of these discoveries. Of the different forms of the tiny organisms, amounting to nearly four hundred, which were at that time distinguished, and all included under the name Infusoria, because first seen in infusions of peppercorns, some only are at the present day reckoned as animals. In many cases it has been ascertained that they are the spores of plants, whilst others again belong to the boundary-land where the animal and vegetable kingdoms are merged.

The presence or absence of movement used to be considered as the most decisive mark of the difference between animals and plants, and, accordingly, all the minute

beings which were seen bustling about in watery media were described and labelled as animals. No movement was found in the higher plants which were studied with the microscope about the same time by Dutch, Italian, and English observers; but, on the other hand, these investigations led to a recognition of the quite special peculiarities of such structures as leaves and stem, wood and pith. These parts of plants appeared under the microscope like honey-combs, which are built up of a

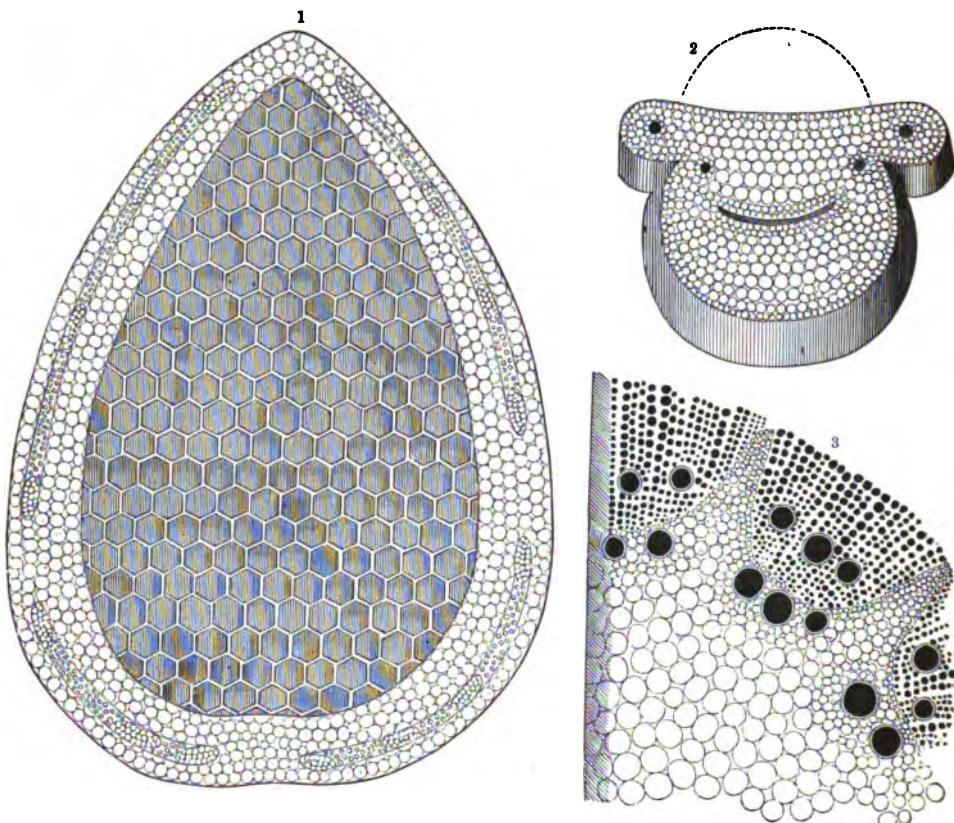


Fig. 4.—Vegetable Cells (from Grew's *Anatomy of Plants*).

<sup>1</sup> Longitudinal section through a young apricot seed. <sup>2</sup> Transverse section of the petiole of the Wild Clary.  
<sup>3</sup> Transverse section of a pine branch.

great number of cells, some empty and some full of honey. From this similarity the term "cell" arose, which later was to play so important a part in botany. In the drawings of parts of plants as seen under the microscope the resemblance to a honey-comb is very apparent; indeed, it is sometimes rather more striking than when seen in reality, as, for instance, is the case in the above reproduction of three engravings from Nehemiah Grew's fine work published in London, 1672. It was also noticed that, besides the structures which resembled honey-comb, there were little tubes and fibres which were distributed and aggregated in very various ways, and were bound up together into strands and membranes, and into pith and wood; further, all these things were seen to increase in size and number in the growing

parts of plants. How growth and multiplication took place, and where exactly the seat of a plant's life lay, remained, of course, obscure. It was, however, natural to assume that the walls of these small cells constituted the essential part and living substance of plants, that they drew materials from the fluids which rose by suction in the tubes, and so increased in size and were renewed.

It was as yet hardly suspected that the slimy substance which filled the cells of a plant, like honey in a honey-comb, was the basis of life. The observation made again and again at the beginning of the nineteenth century, that the cell-contents of certain algae are extruded in the form of globules of jelly, and that each globule moves independently and swims about in the water for a time, but then comes to rest and becomes the starting-point of a new alga, might undoubtedly have led to this conclusion. The accounts of these occurrences were, however, considered incredible by the majority of contemporary observers; and it was not till recently, when Unger established the phenomenon as an indubitable fact, that a proper estimation of its value was accorded. In the year 1826 this botanist investigated under the microscope a water-weed found at Ottakrinn, near Vienna, which had been described by systematic writers as an alga, and named *Vaucheria clavata*. To the naked eye it appears like a dense plexus of dark-green irregularly branched and matted filaments. These filaments, when magnified, are seen to be tubular cells which wither and die away at the base whilst growing at the apex, and developing sac-like branches laterally. (Pl. I.) The free ends of these tubes are blunt and rounded. The substance they contain is slimy, and, though itself colourless, is studded throughout with green granules; whilst near the blunt end of each filament these green particles are so closely packed that the entire contents of that part appear of a dark-green colour.

Now, there comes a time in the life of every one of these filaments when its extremity swells and becomes more or less club-shaped. The moment this occurs, the dark-green contents withdraw somewhat from the extremity, leaving it hyaline and transparent. Almost simultaneously the contents of the swollen part of the tube nearest the apex become transparent, whilst further down the colour becomes very dark. (Pl. I., fig. a.) Twelve hours after the commencement of this change, that portion of the tube's contents which occupies the club-shaped end separates itself entirely from the rest. A little later, the cell-wall at the apex of the tube suddenly splits, the edges of the slit fold back, and the inclosed mass travels through the aperture (fig. c). This jelly-like ball, having a greater diameter than the hole, is at first strangulated as it struggles forward, so that it assumes the shape of an hour-glass and looks for an instant as if it would remain stuck fast. There now arises, however, in the entire mass of green jelly an abrupt movement of rotation combined with forward straining, and in another instant it has escaped through the narrow aperture and is swimming freely about in the surrounding water (fig. d). The entire phenomenon of the escape of these bodies takes place between 8 and 9 A.M., and, in any one case, in less than two minutes. When free, each individual assumes the shape of a perfectly regular ellipsoid (fig. d), having

one pole of a lighter green than the other; it moves always in the direction of the former, so that the lighter end may be properly designated the anterior. At first the ball rises to the surface of the water towards the light, but soon after it again sinks deep down, often turning suddenly half-way round and pursues for a time a horizontal course. In all these movements it avoids coming into collision with the stationary objects which lie in its path, and also carefully eludes all the creatures swimming about in the same water with it. The motion is effected by short processes like lashes or "cilia," which protrude all round from the enveloping pellicle of the jelly-like body and are in active vibration. With the help of these cilia, which occasion by their action little eddies in the water, the whole ball of green jelly moves in any given direction with considerable rapidity. But at the same time as it pushes forward, the ellipsoid turns on its longer axis, so that the resultant motion is obviously that of a screw. It is worthy of note that this rotation is invariably from east to west, that is, in the direction opposed to that of the earth. The rate of progress is always about the same: a layer of water of not quite two centimetres (1·76 cm.) is traversed in one minute. Now and then, it is true, the swimming ellipsoid allows itself a short rest; but it begins again almost immediately, rising and sinking, and resumes its movements of rotation and vibration. Two hours after its escape the movements become perceptibly feebler, and the pauses, during which there is only rotation and no forward motion of the body, become both longer and more frequent.

At length the swimmer attains permanent rest. He lands on some place or other, preferably on the shady side of any object that may be floating or stationary in the water. The axial rotation ceases, the cilia stop their lashing motion and are withdrawn into the substance of the body, and the whole organism, hitherto ellipsoidal and lighter at its anterior end, becomes spherical and of a uniform dark-green colour. So long as it is in motion the gelatinous body has no definite wall. Its outermost layer is, no doubt, denser than the rest; but no distinct boundary is to be recognized, and we cannot properly speak of a special enveloping coat. No sooner, however, is the ball stranded, no sooner has its movement ceased and its shape become spherical, than a substance is secreted at its periphery; and this substance, even at the moment of secretion, takes the form of a firm, colourless, and transparent membrane. Twenty-six hours afterwards, very short branched tubes begin to push out from the interior, and these become organs of attachment. In the opposite direction the cell stretches into a long tube which divides into branches and floats on the water. After fourteen days the free ends of this tube and of its branches swell once more and become club-shaped; a portion of their slimy contents is, as before, separated from the rest and liberated as a motile body, and the whole performance described above is repeated.

## DISCOVERY OF PROTOPLASM.

The study of *Vaucheria* led, then, to the discovery that there are plants which, in the course of their development, pass through a motile stage, propelling themselves about the water as tiny balls of jelly with ciliary processes, and giving exactly the same impression as infusoria. Hand in hand with this discovery went the further observation that a portion of the plastic cell-contents in all plants lies, like a lining, in contact with the inner face of the cell-walls; so that we find that these latter, at a certain stage of maturity, are made up of two layers lying close

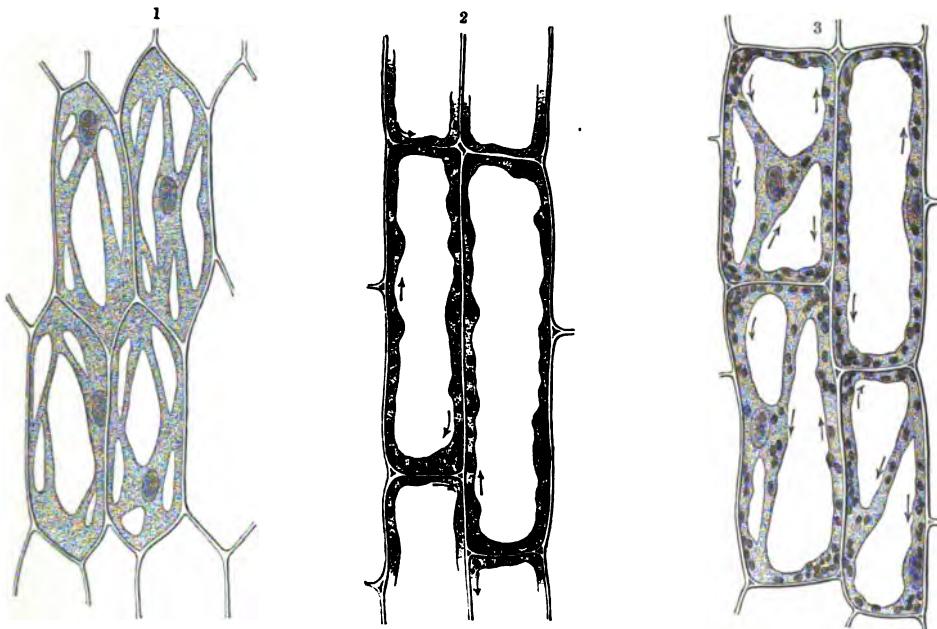


Fig. 5.—Protoplasm inclosed in Cells.

1 Protoplasm in cells of *Orobanche*. 2 Streaming protoplasm in cells of *Vallisneria*. 3 Streaming protoplasm in cells of *Elodea*.

together, the outer one firm and the inner soft. The name of "primordial utricle" was given to this inner layer. On further investigation it turned out that this primordial utricle belongs to a body of gelatinous, slimy consistency which lives in the cell-cavity like a mussel or a snail in its shell. At first it is shapeless and fills the whole cavity with what appears to be a homogeneous mass; but later on it is differentiated into a number of easily-recognizable parts—i.e. into the above-mentioned lining towards the inner surface of the cell-membrane, and into folds, strands, threads, and plates stretching across the interior of the cell. (See fig. 5.) Mohl of Tübingen, the discoverer of these facts, applied in 1846 the name of *protoplasm* to the substance of which the cell-contents are composed.

It is possible for protoplasm, under certain conditions, to exist for a time without any special protective envelope; but, as a general rule, it secretes at once a firm,

continuous coat, and, so to speak, builds itself a little chamber wherein to live. We may therefore distinguish naked protoplasm from that kind which inhabits the interior of a cell of its own creation, and compare the former to a shell-less snail, and the latter to a snail that constructs the house in which its life is spent. Still better may we compare the firm and solid cell-membrane with which the protoplasm clothes itself to a protective coat, a garment fitted to the body; and, following out this analogy, the protoplasm must be designated the living entity in the cell, and the secreted envelope must be considered as merely the skin of the cell. Consequently, although this cell-wall was the part which was first revealed by magnifying glasses, and was called a cell on account of its form, this is not the essential formative element, which has the power of nourishing and reproducing itself. It is the body within the cell, the slimy, colourless protoplasm in full activity within the surrounding membrane made by itself, which must be taken to be the essential part of the cell and the basis of life.

The term cell had become so naturalized in the science that protoplasm which had escaped from a cell-cavity was also called a cell, and the unfortunate name of "naked cell" was brought into use to designate it. More recently many of these older designations have been abandoned as unsuitable. We now include under the term "protoplasts" all these individual organisms, consisting of protoplasm, which occupy little chambers made by themselves, living either alone like hermits or side by side in sociable alliance in more or less extensive structures, able under certain circumstances to leave their domiciles, laying aside their envelopes and swimming about as naked globules.

Only when the protoplasts live in innumerable little cavities congregated close together in colonies, and when these cavities are bounded by even walls and are for the most part uniformly developed in all directions, does the part of a plant composed of them look under the microscope like a honey-comb, and each cavity like a cell. But even in these cases of external similarity there is the essential difference that in a honey-comb each of the walls separating individual cells is common to both the adjacent spaces, and, accordingly, the cells of the comb are like excavations in a continuous matrix; whereas, in sections of cellular plants, every cell possesses its own particular and independent wall, so that in them every partition-wall between neighbouring cavities is composed, properly speaking, of two layers (fig. 6). These two layers are scarcely distinguishable in the case of delicate cell-membranes newly secreted by the protoplasts. Later on, however, they are always to be made out clearly (fig. 6<sup>2</sup>). Frequently the layers separate one from another at certain spots, and thus channels are formed between the cells (fig. 6<sup>1</sup>); these are called "inter-cellular spaces." One often sees cells, too, whose entire surfaces are, as it were, glued together with a kind of cement, and then this substance which is stored between the two layers is called "intercellular substance" (fig. 6<sup>3</sup>).

By loosening the intercellular substance, where present, by mechanical or chemical means, we can easily separate adjacent cells from one another; the two layers of the partitioning cell-walls come asunder, and then each separate cell exhibits a

complete envelope. The individual cell-cavities are often elongated and shaped like either rigid or flexible tubes; or the wall of such a cavity may become very thick and encroach to such an extent on the cavity that the latter is scarcely recognizable. Cells of this kind look like fibres and threads, groups of them look like bundles and strands, and do not resemble even remotely the cells of a honey-comb. The term "cellular" is hence no longer suitable in the case of these structures.

The expression "cellular tissue" is calculated also to occasion a wrong idea of the grouping and connection of the single cell-cavities. By a tissue one would surely understand a collection of thread-like elements so arranged that some of the threads run parallel to one another in one direction, whilst similar threads crossing

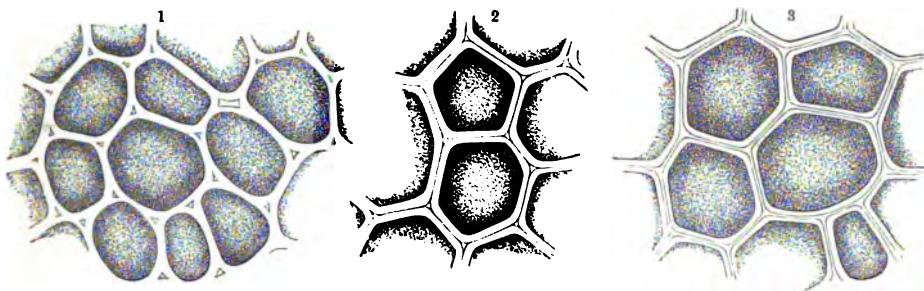


Fig. 6.—Cell-chambers. Showing Intercellular Spaces (1 and 2) and "Intercellular Substance" (3) in the Partition-walls of the Chambers.

the first at right angles are interwoven with them. In such a tissue, as of woven silk or the web of a spider, the threads are held together by intertwining; but this is by no means the case with the collections of cells which have been called cell-tissues. Even where the parts of a so-called tissue of cells are tubular, thread-like, or fibrous, they lie side by side and are joined as it were by a cement, but are never crossed or twisted together like the threads in a woven fabric.

Again, cells have been compared to the bricks of a building, but this analogy is not exact. The process of formation of a cubical crystal from a solution of common salt may perhaps be compared to the piling up of bricks; but when a leaf grows the process is not for one layer of cells to be superimposed from the outside upon another previously deposited. The development of new cells proceeds in the inside of existing cells and ensues from the activity of the protoplasts inclosed within the cell-walls; and these protoplasts not only provide the building materials, but are themselves the builders. It is in this very fact indeed that we grasp the sole distinction between organic and inorganic structures, and on this account especially the above analogy is inadmissible and should be avoided.

Cells and cell-aggregates may be conceived most clearly by considering their analogy to the shells of living creatures, as we have already done more than once in the foregoing pages. Protoplasts are either solitary, inhabiting isolated cell-cavities; or else they live in associated groups, the cells being crowded close together in great numbers and firmly attached to one another—each cavity being inhabited by one such protoplast. When the latter is the case, division of labour usually takes place

in a plant, so that, as in every other community, some of the members undertake one function, some another. The older cells in these plants often lose their living protoplasts, and then, for the most part, serve as an uninhabited foundation to the entire edifice, which may thus be penetrated by air and water channels. The protoplasts have meanwhile erected new stories for themselves and their posterity on the old deserted foundations, and are pursuing their indefatigable labours in the little chambers of these upper stories. This work of the living protoplasts consists in absorbing nutriment, increasing their own substance, maturing offspring, searching for the places which offer most favourable conditions with a view to an eventual transmigration and to colonization by their families; and lastly, securing the region where all these tasks are performed against injurious external influences. The sequence of these labours is always governed by conditions of time and place. Many of them are only to be observed with difficulty in their actual performance and are first recognized in their perfected products, while others are attended by very striking phenomena and are easily followed in their progress.

---

## 2. MOVEMENTS OF PROTOPLASTS.

Swimming and creeping protoplasta.—Movements of protoplasm in cell-cavities.—Movements of Volvocineæ, Diatomaceæ, Oscillariæ, and Bacteria.

### SWIMMING AND CREEPING PROTOPLASTS.

Among the most striking phenomena observed in connection with living protoplasts are, without question, the temporary locomotion of the protoplast as a whole and the displacement and investment of its several particles. The freest motion is of course exhibited by protoplasts which are not inclosed in cell-cavities, but have forsaken their dwelling and are wandering about in liquid media. Their number, as well as the variety of their forms, is extremely great. These naked protoplasts are evolved by several thousands of kinds of cryptogamic plants, at the moment of sexual or asexual reproduction in these plants. The escape from the enveloping cell-wall alone takes place in countless different ways, though the process, as a whole, is conducted in the manner already described in the case of *Vaucheria clavata*. Sometimes a single comparatively large protoplast glides out of the opened cell by itself; at other times, before the cell opens the protoplasmic body divides into several parts—often into a great number—and then a whole swarm of protoplasts struggle out.

These swarming protoplasts differ considerably in form. Usually their outline is almost ellipsoidal or oval; but pear-shaped, top-shaped, and spindle-shaped forms also occur. Often the body of the protoplast is spirally twisted like a corkscrew, and has in addition one end spatulate or clavate. Thread-like processes, definite in number and dimensions and arranged variously, according to the kind of protoplast,

project from the surface of its body. In some instances the whole surface is thickly covered with short cilia, as in *Vaucheria* (fig. 7<sup>1</sup>); in others the cilia form a close ring behind the conical or beak-like end of the pear-shaped body, as in *Oedogonium* (fig. 7<sup>2</sup>); and in others again, one or two pairs of long and infinitesimally thin threads, like the antennæ of a butterfly, proceed from some spot, generally the narrow end (fig. 7<sup>3</sup> and 7<sup>4</sup>). Many forms are provided with a single long lash or flagellum at one extremity (fig. 7<sup>5</sup>), and yet others are spirally wound and are beset with cilia, thus presenting a bristly or hirsute appearance (fig. 7<sup>11</sup>).

These ciliary processes have a combined lashing and rotatory motion, and by their means the protoplasts swim about in water. In many cases, however, swim-

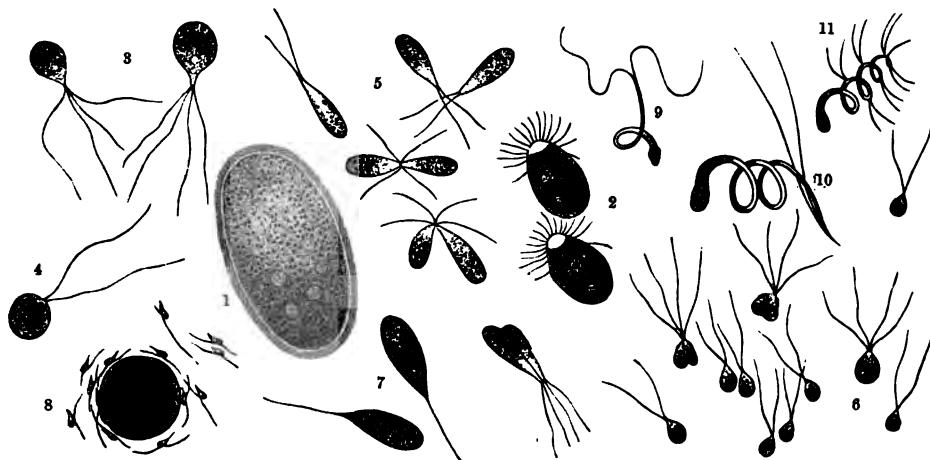


Fig. 7.—Swimming Protoplasm.

<sup>1</sup> *Vaucheria*; <sup>2</sup> *Oedogonium*; <sup>3</sup> *Draparnaldia*; <sup>4</sup> *Colsochete*; <sup>5</sup> and <sup>7</sup> *Botrydium*; <sup>6</sup> *Ulothrix*; <sup>8</sup> *Fucus*; <sup>9</sup> *Funaria*; <sup>10</sup> *Sphagnum*; <sup>11</sup> *Adiantum*.

ming is hardly an appropriate expression; certainly not if one associates the term with the idea of fishes swimming with fins. In point of fact there is, associated with progression in a particular direction, a continuous rotation of the protoplast round its longer axis, and on this account its motion may be compared to that of a rifle-bullet, since in both cases the movement of translation takes place in the direction of the axis round which the whole body spins. The movement in question is not unlike the boring of one body inside another; according to this, the soft protoplasts bore through the yielding water, and by this action make onward progress.

The microscope magnifies not only the moving body, but also the path traversed; and when one contemplates a protoplast in motion, magnified, say, three hundred times, its speed appears to be three hundred times as fast as it really is. As a matter of fact, the motion of protoplasts is rather slow. The swarm-spores of *Vaucheria*, described above, which traverse a distance of 17 millimeters in a minute are amongst the fastest. The majority accomplish an advance of not more than 5 m.m., and many only 1 m.m. per minute.

As was mentioned in the description of *Vaucheria* the locomotion of ciliated protoplasts lasts for a comparatively brief period. It gives the impression of being a journey with a purpose: a search, as it were, for favourable spots for settlement and further development; or else a hunt after other protoplasts moving about in the same liquid. Green protoplasts always begin by seeking the light, but after a time they swim back into the shadier depths. Many of these, especially the larger ones, avoid coming into collision, and are careful to give each other a wide berth. If numbers are crowded together in a confined space, and two collide or their cilia come into contact, the motion ceases for an instant, but in a few seconds they free themselves and retire in opposite directions.

Contrasting with these unsociable protoplasts are others, which have a tendency to seek each other out and to unite; and protoplasm acts in many cases on protoplasm of identical or similar quality, perceptibly attracting it and determining the direction of its motion. It is very curious to watch the tiny pear-shaped whirling protoplasts of *Draparnaldia*, *Ulothrix*, *Botrydium*, and many others, as they steer towards one another and, upon their ciliated ends coming into contact, turn over and lay themselves side by side (fig. 7<sup>5</sup>); or, to see one pursued and seized by another, the foreparts of their bodies brought into lateral contact, and, finally, the two, after swimming about paired for a few minutes, fusing together into a single oval or spherical protoplast (fig. 7<sup>6</sup>). Even the minute fusiform protoplasts which are moved by cilia proceeding from the sides of their bodies (fig. 7<sup>8</sup>), as well as the spirally-coiled forms (figs. 7<sup>9, 10, 11</sup>) endeavour to unite with some other protoplast. They always move towards larger protoplasmic bodies at rest, cling to them closely, and at last coalesce with them into single masses (fig. 7<sup>8</sup>).

As a rule no striking change is to be perceived in the inside of motile protoplasmic bodies during the rotatory and progressive motion caused by their cilia; and the granules and chlorophyll-corpuscles dotted about in the body of the protoplast seem to remain, throughout the period of locomotion, almost unchanged as regards both position and shape. It is only in the vicinity of certain little spaces, called "vacuoles," in the substance of the protoplasm, that changes in many instances are observed, which indicate that, during the motion of the whole apparently rigid mass, slight displacements may also occur in the interior, somewhat in the same way as, when a man walks, the heart inside his body is not still (relatively to the body), but continues to pulsate and cause the blood to circulate. The changes observed in vacuoles have, moreover, been described as pulsations, because they are accomplished rhythmically and manifest themselves as alternate expansions and contractions of the vacant space.

In each of the motile protoplasts of *Ulothrix* (fig. 8) there is found, near the conical end, which is furnished with four cilia, a vacuole which contracts in from 12 to 15 seconds, and dilates again in the succeeding 12 or 15 seconds. In the swarm-spores of *Chlamydomonas* and those of *Draparnaldia* two such vacuoles may be observed close together, whose rhythmic action is alternate, so that the

systole (contraction) of the one always takes place synchronously with the diastole (expansion) of the other. The contraction often continues until the cavity entirely disappears. It must depend, as also does the expansion, on a displacement of that part of the protoplasm which immediately surrounds the vacuole. But such a motion as this in the protoplasmic substance, even if only visible in a small part of the whole body, can scarcely be without its effect on other more distant parts; and it may, therefore, be concluded that the interior of a protoplast, endowed with ciliary motion, rotatory and progressive, does not remain quite at rest relatively, as seems on cursory inspection to be the case.

Protoplasts whose motion is effected by means of cilia have no more need of their vibratile organs when once they have reached their destination. The cilia,



Fig. 8.—Pulsating Vacuoles in the Protoplasm of the large Swarm-spores of *Ulothrix*.

whether numerous or solitary, whether short or long, first of all become stationary and then suddenly disappear. Either they are drawn in or else they deliquesce into the surrounding liquid. Whether the motile protoplasts have come to rest because they have reached a suitable place for further development, as happens in *Vaucheria*, or because they have united, like with like, into a single mass, the form taken by the resulting non-motile body is always spherical. The final act is the development around itself of an investing cell-membrane, so that its soft and slimy substance may be protected by a firm covering from external influences.

Essentially different from the motion just described is that of certain protoplasts which are unprovided with cilia, but perpetually change their outlines, thrusting out considerable portions of their gelatinous bodies in one direction or another, and at the same time drawing in other parts. At one moment they appear irregularly angular, shortly afterwards stellate; then, again, they elongate, become fusiform, and gradually almost round (fig. 9). The protruded parts are sometimes delicate, tapering off into mere threads; sometimes they are comparatively thick, and have almost the appearance of arms and feet in relation to the principal mass. The motion is not in this case like boring, but is best described as creeping. As one or a pair of foot-like appendages is thrown out

in one direction, others on the opposite side are retracted, and the protoplast as a whole glides over the intervening space like a snail without its shell. The analogy is all the more exact since the protoplast, as it glides onward, leaves a slimy trail in its wake, so that the latter is marked by a streak resembling the track of a snail. When two or more of these creeping protoplasts, or plasmodia, meet, they merge into one another, flowing together somewhat in the same way as two oil-drops on water coalesce into one—leaving no distinguishable boundaries between the united bodies. Thus, slimy lumps of protoplasm, which may attain to the dimensions of a closed or open hand, result from the coalescence of great numbers of minute protoplasts. And it is a very remarkable fact that these plasmodia can themselves change their form, putting out lobes and threads, and

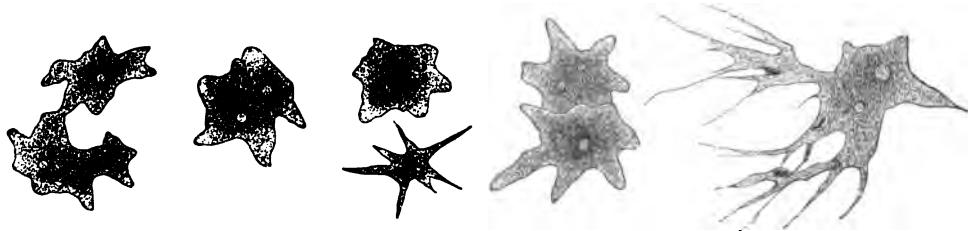


Fig. 9.—Creeping Protoplasm.

creeping about in the same way as the single protoplasts from whose fusion they have arisen.

Creeping masses of jelly sometimes move in the direction of incident light; at other times they avoid light and hide in obscure places, wriggling through the interstices of heaps of bark or into the hollows of rotten trunks; or they may creep up the stems of plants, or glide over the brown earth in a viscous condition. On these occasions they resolve themselves not infrequently into bands, cords, and threads, which surround fixed objects, divide, and combine again, forming a net-work of meshes, or else perhaps frothy lumps like cuckoo-spit. If foreign bodies of small size are enmeshed by the viscous threads of the reticulum, they may be drawn along by the protoplasm as it creeps; and if they contain nutritive material, they may be eaten up and absorbed. Plasmodia are, for the most part, colourless, but some are brightly tinted; in particular may be mentioned the best-known of all plasmodial fungi, the so-called "Flowers of Tan" (*Fuligo varians*), which are yellow, and *Lycogala Epidendron*, which comes out on old stumps of pines, and is vermillion in colour.

#### MOVEMENTS OF PROTOPLASM IN CELL-CAVITIES.

In the case of a protoplast which is not naked, but clothed with an attached cell-membrane, the movements are limited to the space included by the membrane, that is to say to the cell-cavity. Until the protoplasmic cell-body is differentiated into distinct individual portions no very lively motion can in general take place in the coated protoplast; though it is not to be assumed that it abides completely

at rest at any time, except perhaps during periods of drought in summer and of frost in winter, and in seeds during their time of quiescence. This applies particularly to immature cells. In them the protoplast forms a solid body whose substance entirely fills the cell-cavity. The young cell, however, grows up quickly, its cavity is enlarged, and the space, hitherto filled by the protoplast, becomes two or three times as large as before. But the increase of volume on the part of the protoplast itself does not keep pace with the enlargement of its habitation. It is true that it continues to cling closely to the inner face of the cell-wall, thus forming the primordial utricle; but the more central part of its body relaxes, and in it are formed vacant spaces, the vacuoles above mentioned, wherein collects a watery fluid known as the "cell-sap." The portions of protoplasm which lie between the vacuoles resolve themselves gradually into thin partitions bounding them; and lastly, these partitions split up into bands, bridles, and threads, which stretch across the cell-cavity from one side of the primordial utricle to the other, and are woven together here and there where they intersect. With these protoplasmic strands we have already become acquainted.

But the protoplasm in the interior of a growing cell, whilst relaxing and breaking up, also becomes motile if the liquid attains a certain temperature, and then the appearance presented is like that of a lump of wax melting under the action of heat. These movements may be observed very clearly under the microscope in the case of large cells with thin and very transparent cell-membranes, especially when the colourless, translucent, and gelatinous substance of the protoplasm—not always sharply defined in contour—happens to be studded with minute dark granules, the so-called "microsomata." These granules are driven backwards and forwards with the stream, like particles of mud in turbid water, and their motion reveals that of the protoplasm wherein they are embedded. Seeing particles gliding in all directions through the cell-cavity, arranged irregularly in chains, rows, and clusters in the protoplasmic strands, we are justified in concluding that this motion takes place in the substance of the strands itself. The movement, moreover, is not confined to isolated strands, but occurs in all. Granular currents flow hither and thither, now uniting, now again dividing. They often run in opposite directions even when only a trifling distance apart; sometimes two chains are drifted in this way when actually close together in the same band of protoplasm. The streams pour along the primordial utricle and whilst there divide into a number of arms, meeting and stemming one another and forming little eddies; then they are gathered together again and turn into another strand of the more central protoplasm. The individual granules in the currents are seen to move with unequal rapidity according to their sizes; the smaller particles progress faster than the larger, and the larger are often overtaken by the less, and when this happens the result often is that the entire stream stops. If so, however, the crowded particles are suddenly rolled forward again at a swifter pace, like bits of stone in the bed of a river as it passes from a level valley into a gorge. The course of the streaming protoplasm remains throughout sharply marked off from the watery sap

in the vacuoles, and none of the granules ever pass over into the cell-sap from the protoplasm.

Larger bodies, such as the round grains of green colouring-matter or chlorophyll, are in many instances not carried forward, but remain stationary, the protoplasmic stream gliding over them without altering them in any way. Further, the outermost layer of the protoplast, contiguous with the cell-membrane, is not in visible motion in most vegetable cells. On the other hand, occasionally the entire protoplast undoubtedly acquires a movement of rotation, and then the larger bodies imbedded in its substance, *i.e.* chlorophyll corpuscles, are driven along like driftwood in a mountain torrent (fig. 5<sup>2</sup> and 5<sup>3</sup>). On these occasions a wonderful circulation and undulation of the entire mass takes place: chlorophyll grains are whirled along one after the other at varying speeds as if trying to overtake one another; and yet another structure, the cell-nucleus presently to be discussed, is dragged along, being unable to withstand the pressure, and, following the various displacements of the net-work of protoplasmic strands in which it is involved, is at one moment pulled alongside of the cell-wall, at another again is taken in tow by a rope of central protoplasm and hauled transversely across the interior of the cell (fig. 5<sup>3</sup>).

When the rate of the current itself is estimated by the pace at which the granules are driven along, results which vary considerably are obtained, depending chiefly on a qualitative difference in the protoplasm, but secondarily also on temperature and other external conditions. A rise in temperature up to a certain point as a general rule accelerates the rate of the stream. Particles of protoplasm in particularly rapid motion pass over 10 m.m. in a minute; others in the same time traverse from 1 to 2 m.m.; and some, in still less haste, advance only about a hundredth part of a millimeter. Larger bodies, especially the bigger chlorophyll grains, move slowest of all. So it is often hours before chlorophyll grains lying near one side of a cell are pushed through the protoplasm over to the other side, a distance only equal to a small fraction of a millimeter.

The minute granules, as well as the larger grains of chlorophyll and the cell-nucleus, are entirely surrounded by protoplasm; and the protoplasm, whether in the form of bands or threads, whether a peripheral lining or an indefinite mass, must be conceived as always composed of two layers, the outer "ectoplasm" being tougher and denser than the inner "endoplasm," which is softer and somewhat fluid. The former is homogeneous and non-granular, so that it is the more transparent and has the effect of a skin clothing the inner, softer layer, which is granular and turbid. It would be incorrect, however, to think of this as a very strongly-marked contrast, sufficient to mark off one layer clearly from the other. In reality there are no such sharp boundaries, and the tougher ectoplasm passes gradually into the softer and more mobile endoplasm. Of course the granules and corpuscles which one sees drifting in streaming protoplasm are situated within the more yielding endoplasm. It is true, minute particles often appear to glide from one side to the other upon a delicate protoplasmic strand as if it were a tight-rope; but on closer

study it is apparent that the granules which seem to be travelling on the protoplasmic thread are covered by a delicate and transparent protoplasmic pellicle. Thus, these granules imbedded in the substance of protoplasts have no independent motion, but are pushed along by the spreading protoplasm.

Each stream of protoplasm is shut off from its environment and limited by a layer tougher than the rest. But this does not prevent the currents, with their crowds of drifting granules, from changing their direction. In fact we have only to follow for a short time the course of one such granular stream to remark a continuous series of changes: a current from being in a straight line bends suddenly to one side, it broadens and contracts again, now it runs close alongside another channel, now breaks away once more, divides into two little arms, and loses itself finally in the primordial utricle. On the other hand, fresh folds start from the primordial utricle, stretch and grow until they have pushed across the cell-cavity to the other side in the form of bands, or the protoplasm may be drawn out into threads, which elongate until they encounter other similar strings and form a junction with them. The same processes then that are observed in free creeping protoplasts take place to some extent here. Imagine a protoplast captured whilst on its travels—creeping along the level ground—and imprisoned in a completely closed vessel; it would spread itself out over the inner surface of the vessel, would branch and creep about and have just the same appearance as the protoplasts, just described, which inhabit cell-cavities from their earliest youth. This is but the converse of the power possessed by a protoplast set free from its cell, which enables it to move, stretch out, and draw in its various parts, and so to effect locomotion.

Another motion, differing from the creeping, gliding, and streaming action of protoplasts, manifests itself in the so-called swarming of granules contained in the protoplasm. It may be best observed in the cells of the genera *Penium* and *Closterium*, both of which are shown in Plate I., figs. *i*, *k*, though the same phenomenon is to be seen in many allied forms, living in lakes and ponds either singly or congregated in colonies, and remarkable for their bright green colour. The above-mentioned genus *Closterium* includes delicate unicellular forms having a curved or scimitar shape unusual in plants, whence one of its species, in which the semi-lunar form is most striking, has been named *Closterium lunula*. The cell-membrane in all these little water-plants is clear and quite transparent. The greater part of the cell-contents consists of a dark-green chlorophyll body longitudinally grooved; but the protoplasm which is visible in the two sharply tapering ends of the cell-cavity is colourless, and embedded within it is a swarm of microsomata. These granules or microsomata appear to be in a most curious state of motion so long as the protoplast lives. They are to be seen plainly within the limits of the tiny cavity, jumping up and down, whirling, dancing, and rushing about without really changing their position. One is reminded of the apparently purposeless journeys to and fro within reach of their homes of ants or bees, and the movement has been called not inaptly

"swarming." It is difficult to imagine the kind of motion possessed by the protoplasm in which these swarming microsomata are embedded; but however closely it is confined, there must be continual rapid displacements in its substance, which is very fluid, and it may be assumed that here again it is not so much the tiny grains that bestir themselves as the protoplasm which holds them. Probably the protoplasmic matter spreads and stretches out and rotates, and individual granules are carried about by it. This, of course, does not exclude the possibility of the granules possessing a vibratory motion of their own within the mass of protoplasm.

Similar, but not identical, is the swarming movement of protoplasm observed in cells of the Water-net (*Hydrodictyon utriculatum*), and in several other plants allied to it. *Hydrodictyon* looks like a net in the form of a sac, and composed of green threads. The meshes of this net, which are generally hexagonal, consist, however, not of filaments but of slender cylindrical cells joined together by threes at their extremities, somewhat in the same way as are the leaden frames of the little hexagonal panes of glass in gothic windows. The protoplasmic body of one of these cells in due time breaks up into a great multitude (7000–20,000) of tiny clots, which begin to move and swarm within the cell-cavity in what appears to be a disordered medley. In half an hour, however, the excited mass is again restored to rest: the minute particles take form and arrange themselves in definite order, each having two others at either extremity, making an angle of 120° with it; and, lastly, all unite to form a single tiny net having exactly the same shape as the one whose component cell constituted the arena of this process of construction. The miniature water-net so formed then slips out of the cell, the latter opening for the purpose, and in from three to four weeks it grows to the same size as the parent plant.

In the above we have an instance of a protoplast producing a whole colony of cells, which are obliged to leave their home for want of space. In cases previously considered we have found the protoplast stretching and elongating in all directions, drawing itself out into bridles and spreading as a delicate lining to walls, and so endeavouring generally to expand and present the greatest surface possible. Again, we have seen it wandering freely, creeping, swimming, and rotating, and by this method also covering as much space as it can. But, conversely, there is a time when a protoplast tends to the other extreme; the expanded mass of its body gathers itself together again, contracts more and more, and at length becomes a resting sphere, that is to say, it assumes the configuration which exposes the least surface to the environment.

This process exhibits itself with particular clearness within the cell-cavities of the green algae known by the name of *Spirogyra*, a species of which is represented, magnified three hundred times, in Plate I., fig. *l*. In this alga the protoplasm in each mature cell-cavity forms, as a general rule, a very delicate parietal lining wherein green chlorophyll bodies are embedded, arranged in a spiral band. All of a sudden, however, this lining strips itself off the inner

face of the cell-wall and shrinks together so as in a short time to present the appearance of a sphere occupying the middle of the cell-cavity. Again, just as this contraction is an instance of a special form of protoplasmic motion, so also the further change which the contracted protoplast in a cell of *Spirogyra* undergoes is reducible to displacements in its substance, and must be mentioned as a special kind of protoplasmic movement. For the conglomerated protoplast remains but a short time in the middle of the cell-cavity. It leans almost immediately to one side, thrusting itself into a protuberance of the cell-membrane, which is concurrently developed, and which, when further developed, forms a passage leading over into another cell-cavity. Its body becomes longer and narrower, and at last slips through the passage into the next cavity, where a second protoplast awaits it; and the two then unite, fusing together into one mass. It is not premature to remark that all these displacements and investments of the protoplasmic substance in cells of *Spirogyra*, including the phenomena of contraction, as well as those of pushing forward, escape, and coalescence, are not produced as the results of a shock, impulse, or stimulus from without, but are to be looked upon as movements proper to the protoplasm, and resulting from causes inherent in the protoplasm.

#### MOVEMENTS OF VOLVOCINEÆ, DIATOMACEÆ, OSCILLARIAE AND BACTERIA.

Very remarkable is the movement of those wonderful organisms which are comprised under the name of Volvocineæ. One species, *Volvox globator*, was known to so ancient an observer as Leeuwenhoek; but he, and after him Linnaeus, took it to be an animal on account of its extraordinary power of locomotion, and it was named the "globe-animalcule." A *Volvox*-sphere consists of a large number of green protoplasts living together as a family and arranged with great regularity within their common envelope. They appear to be disposed radially, and to be linked together and held firm by a net-work of tough threads, their poles being directed towards the centre and the periphery of the sphere respectively. From the peripheral extremity, which in each protoplast is marked out by a bright red spot, proceed a pair of cilia, and these protrude through the soft gelatinous envelope of the whole sphere, and move rhythmically in the surrounding water. A *Volvox*-globe rolls along in the water propelled by regular strokes, like a boat manned by a number of oarsmen, as soon as the protoplasts, which form the crew of this strange vessel, begin to manipulate their propellers. The effect is exceedingly graceful, and has justly filled observers of all periods with astonishment; indeed no one seeing for the first time a *Volvox*-sphere rolling along can fail to be impressed and delighted.

Another plant allied to the foregoing, the so-called "red-snow," has always excited wonder in no less degree from the remarkable phenomena of motion which it exhibits, but also because of its characteristic occurrence in situations where one

might suppose all vital functions would be extinguished. It was in the year 1760 that De Saussure first noticed that the snowfields on the mountains of Savoy were tinged with red, and described the phenomenon as "red-snow." Once on the look-out for it, people found this red-snow on the Alps of Switzerland, Tyrol, and the district of Salzburg, on the Pyrenees, the Carpathians, and the northern parts of the Ural Mountains, in arctic Scandinavia, and on the Sierra Nevada in California. But red-snow has been seen on the most magnificent scale in Greenland. When Captain John Ross in 1818 sailed round Cape York on his voyage of discovery to Arctic America, he noticed that all the snow patches lying in the gorges and gullies of the cliffs on the coast were coloured bright crimson; and the appearance was so startling that Ross named that rocky sea-shore the "Crimson Cliffs." On the occasion of later expeditions to the arctic regions, red-snow was observed off the north coast of Spitzbergen, and in Russian Lapland and Eastern Siberia, but never in such surprising luxuriance as on the Crimson Cliffs of Greenland.

If a snow-field coloured by red-snow is examined near at hand it is found that only the most superficial layer, about 50 millimeters in depth, is tinged. It is also present in the greatest quantities in places where the snow has been temporarily melted by the heat of summer, particularly therefore in depressions, whether big or little, and towards the edges of the snow-field, where the so-called snow-dust or Cryoconite extends regularly in the form of dark, graphitic smearable streaks. Examined under the microscope, the matter which causes the redness of the snow appears as a number of spherical cells having a rather substantial colourless cell-membrane and protoplasmic contents permeated by chlorophyll. The green colour of the chlorophyll is, however, so disguised by a blood-red pigment that it is only possible to detect it when the latter has been extracted, or in cases where it is limited to a few definite spots in the cell. These spherical cells do not move, and so long as the snow is frozen they show no sign of life. But as soon as the heat of the summer months melts the snow, these cells acquire vitality, visibly increasing in size and preparing for division and multiplication the moment they have attained a certain volume. The growth, so far as it depends on nutrition, takes place at the expense of carbon dioxide absorbed by the melted snow from the atmosphere and of the inorganic and organic constituent parts of the dust. We shall frequently have occasion to return to this dust, but at present it is only necessary to observe, for the comprehension of the drawing of red-snow as seen under the microscope (Pl. I., figs. *e-h*), that in the Alps, amongst the organic materials which constitute the dust, pollen-grains of conifers occur with great frequency, especially those of the fir, arolla, and mountain pine. These pollen-grains have been swept up into the high Alps by storms, and are already partially decayed. In all the material that I investigated I found the red-snow cells mixed with pollen-grains of the above-mentioned conifers. The pollen-grains are oval in cross-section, of a dirty yellow colour, and swollen laterally into two hemispherical wings, as is shown in Pl. I., figs. *e-h*.

As has been stated, the red cells are nourished by the constituent elements of

the dust, which are dissolved in the melted snow. They grow and at last divide so as to form daughter-cells, usually four in number but often six or eight and less frequently two only (Pl. I., fig. *f*, *g*). As soon as the division is accomplished, the daughter-cells, so produced, free themselves, assume an oval shape, and display at their narrower extremity two rotating cilia by means of which they move about in snow-water with considerable vivacity. The interstices of the still unmelted, but now granular, snow, are filled with water from the melted parts, and through these the red cells swim away and are thus diffused over the snow-field. At the moment of escape and first assumption of movement the cell-body appears to be uninclosed. But it soon clothes itself with an extremely delicate, though clearly discernible skin, which, curiously enough, does not lie close to the protoplasm, which is withdrawn slightly and inclosed as in a distended sac (see Pl. I., fig. *e*). Only in front, where the two cilia carry on their whirling motion, does the skin lie close to the body of the cell; and it must be presumed that the cilia, which are simply extensions of the protoplasmic substance, are projected through the envelope. The swarm-spores afford an example of an unusual type of protoplasts, namely of those that move about singly in the water by means of cilia and at the same time carry their self-made cell-membranes with them.

How long the motile stage lasts under natural conditions has not been determined for certain. On the mountains of central and southern Europe, where hot days are followed, even in the height of summer, by bitterly cold nights, causing the melted snow which has not run off to freeze again in the depressions of the snow, the movement no doubt is often interrupted. On the other hand, in high latitudes, where the summer sun does not set for weeks together, such interruption would be exceptional. In any case, however, the locomotion of the red cells with their hyaline cell-membranes is not limited to so short a period as is that of naked ciliated protoplasts. Moreover they have the power of nutrition and growth like the red resting-cells from which they originate, and they have been observed, in a culture, to increase in size fourfold within two days. When at last they come to rest they draw in their cilia, assume a spherical shape, thicken their cell-membrane, which now once more lies close to the protoplasmic body, and divide anew into two, four, or eight cells (Pl. I., fig. *f*, *g*). The fusion of the protoplasts of the red cells in pairs, and their sexual propagation, which has been observed in addition to the above-described asexual multiplication, will be the subject of discussion later on. At present we need only add with reference to this remarkable plant that it was named *Sphaerella nivalis* by the botanist Sommerfelt, and that not only in mode of life, but also in form and colour, it most closely resembles a kind of blood-red alga, which makes its appearance in Central Europe in little hollows temporarily filled with rain-water in flat rocks and slabs of stone, and also inside receptacles exposed to the open. This alga has received the name of *Sphaerella pluvialis*, and also that of *Hæmatococcus pluvialis*.

Lastly, we have to consider the mysterious movements exhibited by many Diatomaceæ, and by the filamentous species of *Zonotrichia*, *Oscillaria*, and

*Beggiatoa*. As regards the Diatoms, some of them are firmly attached to a support, and are not generally capable of locomotion; but others are almost incessantly in motion, and these little unicellular organisms steer themselves about with great precision near the bottom of the pools of water in which they live. Their cell-membrane is transformed into a siliceous coat, and this coat, which is hyaline and transparent, but very hard, consists of two halves shutting together like the valves of a mussel. The entire cell thus coated has the form of a gondola or little boat, with a keel either straight or curved (*Pleurosigma*, *Pinnularia*, *Navicula*), and is provided with various bands, ribs, and sculpturings on its siliceous walls. Driven by inherent forces, these little protected cruisers pursue their way at the bottom of the water or over objects which happen to be in the water. They either glide evenly over the substratum, or else proceed by fits and starts at rather long intervals, and apparently with difficulty. For some time they may hold a straight course, but not infrequently they deviate sideways without apparent cause, and after deviating return again. They double round projecting objects or push them out of the way with one of their hard points, which are often thickened into nodules, and cause the obstructing objects to slip by alongside the keel of the little vessel. Yet no paddles or cilia are to be seen projecting from it, as in the case already described of *Volvocineæ*; nor does the siliceous coat exhibit any sort of motile processes whereto the movements might be attributed. But the strong analogy between the structure of these Diatomaceæ and that of mussels seems to justify the assumption that the two siliceous valves, which are fast shut during the period of rest of the Diatoms in question, move a little apart, so that the protoplast living within can push out one edge of its body and creep along over the substratum by means of it.

The movements of the filaments of *Beggiatoa*, *Oscillaria*, and *Zonotrichia* are explained in a similar manner. These filaments are made up of a number of short cylindrical or discoid cells, and are attached by one end, but with the other execute most striking movements. They stretch themselves and then contract again, coil up and straighten out like snakes, and, most characteristic of all, make periodic oscillations in the water. The belief is that the mechanism of this motion is similar to that of the preceding, that infinitesimally fine filaments of protoplasm inserted spirally penetrate the cell-walls, and that these act like the propeller of a ship.

On looking back over the multifarious examples of movement that have been described, the conviction that the capacity for motion is inherent in all living protoplasts is difficult to resist. In many cases, of course, the displacement and replacement of the substance no doubt takes place so slowly that it is scarcely possible to express its amount numerically. Movement may even entirely cease for a time; but, as necessity arises, and under favourable external circumstances, the protoplasmic mass always becomes mobile again—the direction of its motion being determined by inherent forces. There is still much to learn, no doubt, concerning the objects and significance of the different movements of protoplasm;

but in this connection we are justified in assuming that all these movements have to do with the maintenance and multiplication of the protoplasts. For instance, amongst the objects of the various movements are the search for food, the elimination of useless material, the production of offspring, the discovery of the rays of sunlight necessary to the existence of chlorophyll-bodies and of suitable spots to colonize. This conception has been brought out frequently in the course of the foregoing description, and will again engage our attention in succeeding pages.

---

### 3. SECRECTIONS AND CONSTRUCTIVE ACTIVITY OF PROTOPLASTS.

Cell-sap.—Cell-nucleus.—Chlorophyll-bodies.—Starch.—Crystals.—Construction of the Cell-wall and Establishment of Communication between Neighbouring Cell-cavities.

CELL-SAP.—CELL-NUCLEUS.—CHLOROPHYLL-BODIES.—STARCH.—CRYSTALS.

In addition to the powers which the living protoplast possesses of shifting its parts, of expanding and contracting, of dividing and of fusing like with like, it has also the properties of adapting different parts of its body to particular functions, of building up various chemical compounds, and of separating them out when necessary. As the protoplast stretches and expands, spaces and depressions arise within it, and these form ultimately, when the protoplast is limited to a peripheral layer lining the walls of the cavity, a single central vacuole. In the spaces there is secreted, in the first instance, the cell-sap, a watery fluid containing a variety of substances either suspended or in solution, of which the chief are sugar, acids, and colouring matters. Moreover, in the interior of the protoplasm itself, structures with quite different forms occur, and are easily recognizable by their contours; these are the cell-nucleus, chlorophyll-bodies, and starch-grains.

The principal feature of the cell-nucleus is that, although the substance of which it is composed is only slightly different from the general protoplasm of the cell, yet it is always clearly marked off from the protoplasm. In the undeveloped protoplast the nucleus is usually situated in the middle, but in mature protoplasts it is either pressed against one wall of the cell or suspended in a sort of pocket of protoplasmic filaments in the interior (fig. 5<sup>1</sup> and 5<sup>8</sup>). It may be pushed along by the streaming protoplasm and dragged into the middle of the cell, and in that case its shape is sometimes altered and it becomes for a time somewhat elongated and flattened. The nuclear substance, which, as has been already mentioned, differs but little from ordinary protoplasm, is colourless, and studded with microsomata, and is liable to internal displacements similar to those of the entire cell-body. When a protoplast divides, the nucleus plays a very

important part in the process, and it will be necessary later on to discuss its significance in this connection.

The chlorophyll-bodies, mentioned already more than once incidentally, are green corpuscles, roundish, ellipsoidal, or lenticular in shape, and grouped in a great variety of ways (Pl. I., figs. *i*, *k*, *l*, *m*, *p*). They are produced generally in great numbers by the protoplast in special sac-like excavations in its body, but nowhere except where they are necessary, that is, in those cells wherein the transmutation of inorganic food-stuffs into organic matter takes place. This transformation, so important to the existence of the organic world, will be considered in detail later on. Chlorophyll-corpuscles are not, as regards their material basis, essentially different from the substance of the protoplasm in which they are formed, and in which they remain embedded for life, but their green colour distinguishes them very clearly from their environment. This greenness is due to a colouring matter stored in the protoplasmic substance of the corpuscle; and our ideas of plant-life are so intimately associated with this remarkable pigment, that a plant that is not green seems to us to be almost an anomaly.

Besides the nucleus and the chlorophyll-bodies or corpuscles, protoplasts produce starch-grains, aleurone-grains, crystals of oxalate of lime, and drops of oil, all of which will be dealt with presently in their proper place. They are evolved in accordance with the requirements of the moment and with the position held in the edifice of the plant by the cells concerned. Moreover, the walls of the cells themselves are the work of the protoplasts, and it is not a mere phrase, but a literal fact, that the protoplasts build their abodes themselves, divide and adapt the interiors according to their requirements, store up necessary supplies within them, and, most important of all, provide the wherewithal needful for nutrition, for maintenance, and for reproduction.

#### CONSTRUCTION OF THE CELL-WALL AND ESTABLISHMENT OF CONNECTIONS BETWEEN NEIGHBOURING CELL-CAVITIES.

Of all these performances, the construction of the cell-wall shows the greatest variety from the nature of the case. For the envelope with which each individual protoplast surrounds itself serves at once as a protection for the delicate protoplasm, and as a firm support for structural additions; and, at the same time, it must not impede the reciprocal action between the protoplasts and the external world, or the intercourse between those living in adjoining cavities. These cell-walls are accordingly very wonderful structures, and we shall often have occasion to discuss them, especially with reference to the significance of variations in their structure in particular cases. At present it is sufficient to remark that the original envelope which is secreted from the body of a protoplast and which appears at first as a delicate skin, is made of a substance composed of carbon, hydrogen, and oxygen, belonging to the class of carbohydrates.

The name of cell-membrane, usually applied to the original envelope formed by

the cell-body, is one quite suitable for the purpose. But this earliest covering undergoes many modifications. The protoplast is able to store up in it suberin, lignin, silica, and water in greater or smaller quantities, and by this means it either makes the envelope more flexible than it was in the first instance, or else hard and stiff, converting it into a shell-like case. Even the shape is seldom preserved as it was originally. The solitary protoplast surrounded by its cell-membrane is generally in the form of a roundish ball, and its envelope, which is closely adherent, exhibits a corresponding configuration. Young cells, aggregated together, have outlines too which remind one of crystalline forms, such as dodecahedra, cubes, and short six-sided prisms. But when a protoplast has produced its first delicate covering it does not come to rest, but goes on working at the membrane, distending and thickening it, transforming a cavity which was originally spherical or cubical into one of cylindrical, fibrous, or tabular shape, and strengthening its walls with pilasters, borders, ridges, hooks, bands, and panels of various kinds. Where a number of protoplasts work gregariously at one many-chambered edifice, cells of most diverse forms are produced in close proximity to one another. These varieties are, however, never without method and design, but are invariably such as to adequately equip each cell for the position it holds and for the particular task allotted to it in the general domestic economy.

The volume attained by cell-cavities in consequence of the expansion of their walls varies within very wide limits. The smallest cells have a diameter of only one micro-millimeter, *i.e.* the thousandth part of a millimeter; others, as for example yeast-cells, measure perhaps two or three hundredths of a millimeter; and yet others have outlines perceptible to the naked eye and have a volume amounting to one cubic millimeter. Tubular and fibrous cells often stretch longitudinally to such an extraordinary extent that some with a diameter of scarcely the hundredth part of a millimeter reach a length of one, two, or even as many as five centimeters. An instance may be seen in the filaments of *Vaucheria clavata* (Pl. I., figs. *a-d*), and again in the fibrous cells from which our linen and cotton fabrics are manufactured.

The enlargement of a cell-cavity, or, in other words, the growth in area of its walls, ensues in consequence of the intercalation of fresh particles between those which, by their mutual coherence, form the delicate skin of the protoplast—the earliest stage of the cell-wall. When these intercalated particles are situated in the same plane as are those already deposited, the cell-wall resulting from this method of construction will increase in area without adding to its thickness. But when once the cells are full-sized, the constructive activity of the protoplasts has to be directed in many cases to the strengthening and thickening of their walls, so that later on they may be able to perform special duties. From the appearance of this thickening one would judge that a number of layers were deposited on the thin original wall according to requirement, and in many instances no doubt the process corresponds to this appearance; but, as a rule, the thickness of the wall is increased by intercalation, on the part of the protoplasts, of

additional material between the original particles, a process which has been termed "intussusception."

The appearance of stratification in thickened cell-walls is naturally most striking where substances of different kinds have been deposited alternately in the different parts of the wall, and when successive layers take up unequal quantities of water. The thickening may at length result in such an extreme restriction of the cell-cavity that its diameter is less than that of the inclosing wall. Sometimes nothing remains of the cavity but a narrow passage, and then the cells are like solid fibres. Formerly they would not have been classed with cells at all, but would have been distinguished under the name of fibres, from the forms resembling honey-comb cells. The protoplasts in these contracted cells languish and often die, especially when the walls of the self-made prison are greatly thickened and do not allow of intercourse with the world outside. But generally a protoplast takes care, in constructing its dwelling, not to close itself in entirely, nor to cut itself off permanently from the outer world. It either makes from the very beginning little windows in the walls of its house, leaving them quite open or closed only by thin, easily-permeable, membranes; or else, after constructing a completely closed envelope, it redissolves a piece of it, thus making an aperture through which in due time it is able to effect its escape. The scope of this work does not admit of an exhaustive treatment of the formative power possessed by protoplasts needful for these results; it will be sufficient to give a general description of some of the more important processes which have for their object the establishment of a connection between adjacent cell-cavities and of communication with the external world.

The new particles of material, or cellulose, which are to strengthen the delicate original cell-membrane, are in many instances not deposited or intercalated evenly over the entire surface of the protoplast. Little isolated spots are left unaltered, and these may be compared in a way to the small glazed windows in a living-room, or cabin port-holes closed by thin panes of glass. The part of the thickened wall which immediately surrounds the little window, and which so to speak constitutes its frame, has, besides, often a very characteristic structure, being elevated so as to form first a ring-like border, and eventually a hood, arching over the window and perforated in the middle (see fig. 10<sup>1</sup>). A comparison of this structure, arched over the thin spots in a cell-wall, to the iris spread in front of the crystalline lens in an eye would be still more appropriate. A similar annular border projects likewise from the window-frame on the other side, facing a neighbouring cell-cavity, so that the window appears symmetrically vaulted on both sides by mouldings with round central apertures (fig. 10<sup>2</sup>). Supposing someone wanted to pass from one cell-cavity to the other he would have in the first place to go through the hole in the moulding on his side. He would then find himself in a roomy space, which we will call the vestibule, and would next have to break through the little window, which is somewhat thickened in the middle, but elsewhere is as soft and thin as possible. On the further side

again would be a vestibule, and it would not be until he had emerged from this through the aperture in the second moulding that he would reach the interior of the adjoining cell. Seen from in front, the outline of one of these windows, or rather the outline of the common floor of the vestibules, appears as a circle, whilst the aperture or opening in the moulding—which is exactly in the centre of this circle—is seen as a bright dot or pit encompassed by the circle which defines the limits of the vestibule. Hence these curiously protected window structures are named bordered pits. They are shown in fig. 10<sup>1</sup> and 10<sup>2</sup>, and are to be seen in great perfection in the wood-cells of pines and firs.

Whenever bordered pits are formed, the thickening of the cell-membrane is comparatively slight; the frame of the window in the cell-wall is never more than

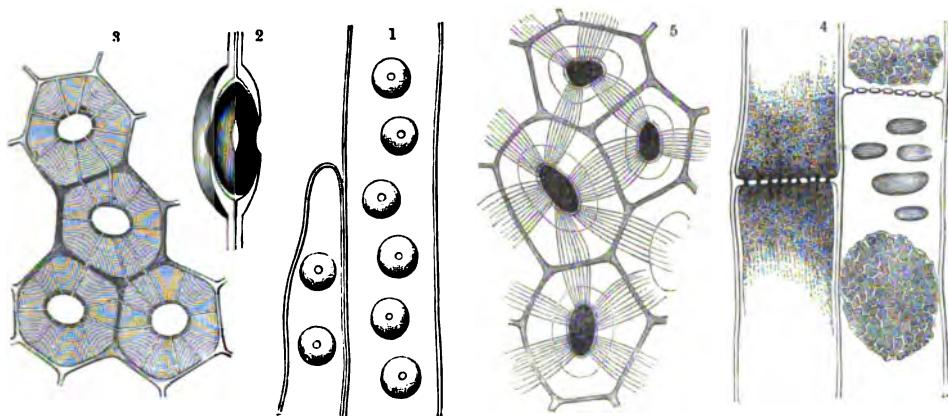


Fig. 10.—Connecting Passages between adjacent Cell-cavities.

<sup>1</sup>, Bordered pits. <sup>2</sup>, Section of a bordered pit. <sup>3</sup>, Mode of connection of adjacent cells in the bundle-sheath of *Scolopendrium*. <sup>4</sup>, Sieve-tubea. <sup>5</sup>, Group of cells from seed of *Nux-vomica*, the protoplasts of adjoining cell-cavities connected by fine protoplasmic filaments.

five times as thick as the window-pane itself. In other cases, however, the cell-wall becomes twenty or thirty times as thick as it was at first, and the interior of the cell is thereby seriously diminished in size. But even if, little by little, the cell-wall augments in thickness a hundredfold, any spot where thickening has not taken place from the first, and where, accordingly, a little depression occurs, is not subsequently covered with cellulose, but is carefully kept open by the protoplast as it builds. A greatly thickened wall of this kind resembles a fortification provided here and there with deep, narrow loopholes. Where two cells thus provided adjoin one another, the windows in the one occur, normally, exactly opposite those of its neighbour, and the result is the formation of canals, very long relatively, which penetrate through the two adjacent cell-walls and connect the neighbouring cell-cavities together (fig. 10<sup>3</sup>). A canal of this kind is still closed, it is true, in the middle by the original cell-membrane as though by a lock-gate; but this slight obstruction may be removed later by solution, and the contiguous cells have then perfectly open connection through the canal.

Very frequently provision is made in the very first rudiments of a cell-mem-

brane, destined to constitute a partition-wall, for open communications such as the above. For segments of the wall of various sizes are made from the beginning with sieve-like perforations, as is shown in fig. 10<sup>4</sup>, which represents diagrammatically portions of tubular cells called "sieve-tubes." The pores are crowded close together on the perforated areas of the walls of the sieve-tubes, and their dimensions are relatively broad and short. Thus, when two neighbouring protoplasts reach out to one another through these pores, that is to say, when there is continuity of the protoplasm of the two cell-cavities, the connecting filaments, which pass through the pores and which fill them completely, are short and thick and have the appearance of pegs or stoppers.

But in many cases the pores through which adjoining cell-cavities communicate are drawn out to a great length, forming infinitesimally slender passages. They are situated close together in great numbers and penetrate transversely through the thick cell-walls (fig. 10<sup>5</sup>). Neighbouring protoplasts may be brought equally well into mutual connection by means of these canals, or perhaps it would be better to say that their connection may be equally well maintained. For it is very probably the case that in the first rudimentary partition-wall, which is produced between the products of division of a protoplast, minute spots remain open and are occupied by connecting threads common to both halves of the protoplasm as they draw apart. Then in proportion as the partition-wall between the two protoplasts, produced by the division, becomes thicker, the openings take the form of fine canals, and the connecting filaments are modified into long and exceedingly fine threads which fill the canals. These protoplasmic threads pierce through the thickened cell-wall in the same way as a dozen telegraph-wires might be drawn through a partition from one room into another. Often a number of protoplasts living side by side and one above the other are linked together by filaments of this kind, which radiate in all directions.

This species of connection, of which an intelligible idea is given by fig. 10<sup>5</sup>, escaped the notice of observers in former times owing to the extraordinary minuteness of the canals, and delicacy of the protoplasmic filaments. Another method of communication between protoplasts in adjoining cells has, on the other hand, been long known and often described, its phenomena being very striking and visible when only slightly magnified. The connection referred to is that which is afforded by the formation of so-called "vessels." By vessels the older botanists understood tubes or utricles, arising from the dissolution of the partition-walls between a series of cells. Either the partition-walls in a rectilineal row of cells vanish, in which case long straight tubes are produced; or portions of the walls of cells arranged at different angles to one another are dissolved, and then tubes are formed having an irregular course, and sometimes branching or even uniting, so as to make a net-work. In instances of the first kind the lateral walls of the series of cells which are to lose their transverse partitions are previously thickened and made stiff by the protoplasts, which also provide them with various mouldings and panellings, and above all with bordered pits. This task accomplished, the protoplasts forsake the tubes, whose

function thenceforth it is to serve as passages for air and water; thus the continued presence of the protoplasts is no longer advantageous. On the other hand, in the second class of vessels the lateral walls of the cells, which have coalesced to form them, exhibit no thickening, but are soft and delicate, and resemble flexible tubing. These tubes, moreover, are not deserted by their protoplasts; but, after the coalescence of a number of cells into a single duct has taken place, the protoplasts in the cells are themselves merged together, and the entire tube is then occupied by an uninterrupted mass of protoplasm, which generally persists as a lining to the wall.

As the initiation and construction of cell-walls are the work of the living protoplast, so also is their removal. The home it has made for itself the protoplast can also demolish—either partially or completely. But this demolition is preluded by the importation of particles of water into the portions of the wall which are to be destroyed. The introduction of water brings the wall into a gelatinous condition; the cohesion of its constituent particles is loosened, little by little, and at length completely abolished.

---

#### 4. COMMUNICATION OF PROTOPLASTS WITH ONE ANOTHER AND WITH THE OUTER WORLD.

The transmission of stimuli and the specific constitution of protoplasm.—  
Vital Force, Instinct and Sensation.

##### THE TRANSMISSION OF STIMULI AND THE SPECIFIC CONSTITUTION OF PROTOPLASM.

As has been already intimated, the breaking down of individual cell-walls and the formation of the various pits, sieve-pores and fine canals in thickened membranes, in the manner described in preceding pages, are processes of great importance to the life of protoplasts. In the first place, many of the resulting structures are the means of preserving the possibility of intercourse with the outside world. In a space inclosed by evenly thickened walls, the absorption of air, water, and other raw materials from the environment would be very difficult if not impossible; the protoplast inside would soon lack the provisions needful for further development, and would at last die of starvation, drought, and suffocation. But the little windows, whether open or closed by thin permeable membranes, enable it to supply itself with all necessities of life. Another advantage is derived, in the case of many of these structures, inasmuch as the protoplasts on occasion escape through the open doors and settle down in some other part of the cell-colony, where they are able again to make themselves useful. Lastly, one of the most important benefits of all is due to the fact that mutual intercourse between protoplasts, living together as a commonwealth, is rendered possible by the canals which join them together. And

such an intercourse must of necessity be presumed to exist. When one considers the unanimous co-operation of protoplasts living together as a colony, and observes how neighbouring individuals, though produced from one and the same mother-cell, yet exercise different functions according to their position; and, further, how universally there is the division of labour most conducive to the well-being of the whole community, it is not easy to deny to a society, which works so harmoniously, the possession of unity of organization. The individual members of the colony must have community of feeling and a mutual understanding, and stimuli must be propagated from one part to another. No more obvious explanation offers than that the protoplasmic filaments, which run like telegraph-wires through the narrow pores and canals in the cell-walls (see fig. 10<sup>5</sup>), serve to propagate and transmit stimuli from one protoplast to another. These threads of protoplasm may indeed be likened to nerves which convey impulses determining definite actions from cell to cell.

Imagination takes us further still, and raises the cell-nucleus to the position of the dominant organ of the cell-body. For the nucleus not only determines the activity of the individual protoplast within its own cavity, but continues in sympathetic communion with its neighbour by means of all the threads and ligaments which converge upon it. This last idea in particular derives support from indications that the filaments uniting neighbouring protoplasts have their origin in specific transformations in the substance of the nucleus itself. When a protoplast living in a cell-cavity is about to divide into two, the process resulting in division is as follows:—The nucleus places itself in the middle of its cell, and at first characteristic lines and streaks appear in its substance, making it look like a ball made up of threads and little rods pressed together. These threads gradually arrange themselves in positions corresponding to the meridian lines upon a globe; but, at the place where on a globe the equator would lie, there then occurs suddenly a cleavage of the nucleus—a partition-wall of cellulose is interposed in the gap, and from a single cell we now have produced a pair of cells. In this way, from the nucleus, and from the protoplast of which the nucleus is the centre, two protoplasts have been produced, each having a nucleus of its own, and they thenceforth live side by side, each in its own chamber. It has been proved that in this process of division the substance of the nucleus is not completely sundered by the partition as it grows, but that, as we have already mentioned, minute pores are kept open in the cellulose wall, and that the pair of protoplasts continue joined together by threads running through these pores.

When we realize that every plant was once only a single minute lump of protoplasm, inasmuch as the biggest tree, like the smallest moss, has its origin in the protoplasm of an egg-cell or a spore; and when we consider how, by growth and repeated bipartition, thousands of cells are evolved, step by step, from a single one, whilst their protoplastic bodies still remain united by fine filaments, we arrive of necessity at the conclusion that the whole mass of protoplasm, living in all the myriads of cells whose aggregation constitutes a tree, really is, and

continues to be, a single individual, whose parts are only separated by perforated sieve-like partitions. Every member of this community occupies a particular compartment or cavity, and is governed by a central organ, the cell-nucleus; but being linked to its fellows by connecting threads of protoplasm, a mutual understanding is thus established among them.

The physical basis of such an understanding may in this manner be represented with tolerable certainty. But it is extremely difficult to throw light upon the process of this mutual intelligence, the actual method whereby the cell-nuclei not only govern within their own narrow spheres, but also co-operate harmoniously for the good of the whole. And yet the problem involved in this unanimity of action, with a view to a systematic development of the plant in its entirety, is of such extreme importance that we cannot evade it even if, in the endeavour to solve it, we have to move altogether in the region of hypothesis.

In every attempt at explanation of the kind we must, at all events, bear in mind that the agreement in question, as well as the processes which take place in pursuance of this agreement, such as the nutrition, growth, and the organization of the entire plant, are reducible to the subtlest atomic agencies in the living protoplasm. They may be resolved into the motion of minute particles, into attractions and repulsions, oscillations and vibrations of atoms, and into re-arrangements of the atomic groups called molecules. Again, these movements are the result of the action of forces, especially of gravity, light, and heat. As regards gravity and light, experiment shows, however, that, when acting on living protoplasm, they give rise to varying effects even under the same conditions; and this fact, which will be discussed frequently later on, indicates that these forces are at any rate only to be conceived as stimulative and not coercive, and that they have no power to determine the kind of form. It is characteristic of the processes set up by gravity and light, especially when they take place in the continuous protoplasm of a great cell-community, that the coarser movements visible to the naked eye are often manifested in members comparatively remote from the part immediately affected by the stimulus. We cannot well represent this to ourselves except by supposing that the stimulus, which is the cause of the movement, is propagated through the threads of protoplasm from atom to atom, and from nucleus to nucleus. But the great puzzle lies, as already remarked, in the circumstance that the atomic and molecular disturbances occasioned by such stimuli and transmitted through the connecting filaments are not only different in the protoplasm of different kinds of plants, but even in the same plant they are of such a nature, according to the temporary requirement, that each one of the aggregated protoplasts in a community of cells undertakes the particular avocation which is most useful to the whole, the effect of this joint labour conveying the impression of the presence of a single governing power of definite design and of methodical action.

That a stimulus causes different occurrences in different species of plants, and more especially, that cell-communities arising from different egg-cells develop into

different forms, though under identical conditions and subjected to the same stimuli, are phenomena which have parallels in the inanimate world. A different sound is produced by striking the key of a piano which is connected to an A-string from that resulting from the transmission of a similar impulse to an F-string; and the difference depends on a difference of structure and an inequality of tension in the strings. Again, solutions of the sulphate and of the hyposulphite of sodium in similar glass vessels are indistinguishable at sight, both being colourless and transparent. These solutions will preserve their liquid condition when cooled down gradually to below freezing-point if they are kept absolutely still; but the moment the vessels are touched and a vibration thereby transmitted to the contents, they freeze. Crystals are formed in the apparently identical liquids, but crystals of different kinds, Glauber's salts in the one case, hyposulphite of sodium in the other. The variety of form depends simply on the sort of atoms, and on their number and mode of grouping.

In a similar manner must be explained the variety of forms in many plant-species developed under the same conditions and affected by the same stimuli. Dozens of kinds of unicellular Desmids and Diatoms are often developed at the same time in a single drop of water in close proximity to one another. Although the protoplasm in the spores of these different species is absolutely identical to our vision, aided by the best microscopes, yet the mature cells exhibit a multiplicity of form which is quite astonishing to the observer on first inspection. One cell is semi-lunar, another cylindrical, a third stellate, a fourth lozenge-shaped, and a fifth acicular. In one specimen the cell-membrane is smooth, in another it is beaded; some are provided with siliceous coats, whilst others have flexible envelopes.

The same thing holds good with respect to the vegetable structures, which are composed of myriads of cells, and develop into huge shrubs or tall trees. The protoplasm in the egg-cell of an oleander is produced close to that of a poplar on the same river-bank, and under exactly the same external conditions. The cells divide, and partition-walls are introduced in the proper direction in either case, according to a plan of structure which is adhered to with marvellous precision by the protoplasts engaged in the work of construction. In each species, stem, branches, foliage, and blossoms have invariably a particular form and arrangement, have the same colour and smell, and contain the same substances. How utterly different are the mature leaf, the opened flower, and ripe fruit of the oleander from the corresponding parts of a poplar. Yet both were nourished by the same earth, were surrounded by the same atmosphere, and encountered the same rays of sunshine. We cannot otherwise explain it than by the supposition that, in a case like this, the difference of form in the perfected state is based upon a difference in the self-developing protoplasm, and that the atoms and molecules of this protoplasm, which appears to us to be uniform, vary in kind, number, and grouping in the two species of plants. Consequently, we must assume that every vegetable organism, every species of plant that appears invariably in the same external form when mature, and develops according to an invariable plan, has a protoplasm

of its own of a certain specific constitution. And, further, we must assume that this specific protoplasmic constitution is transmitted from one generation to another, so that the protoplasm of the oleander, for example, had exactly the same constitution thousands of years ago as it has to-day. Lastly, we must assume that each special kind of protoplasm has the power to reproduce its like, ever anew, from the raw materials occurring in its environment.

#### VITAL FORCE, INSTINCT, AND SENSATION.

The phenomena observed in living protoplasm, as it grows and takes definite form, cannot in their entirety be explained by the assumption of a specific constitution of protoplasm for every distinct kind of plant; though this hypothesis will again prove very useful when we inquire into the origin of new species. What it does not account for is the appropriate manner in which various functions are distributed amongst the protoplasts of a cell-community; nor does it explain the purposeful sequence of different operations in the same protoplasm without any change in the external stimuli, the thorough use made of external advantages, the resistance to injurious influences, the avoidance or encompassing of insuperable obstacles, the punctuality with which all the functions are performed, the periodicity which occurs with the greatest regularity under constant conditions of the environment, nor, above all, the fact that the power of discharging all the operations requisite for growth, nutrition, renovation, and multiplication is liable to be lost. We call the loss of this power the death of the protoplasm. It ensues upon assaults from without if they succeed in destroying the molecular structure so entirely as to render reconstruction impossible; but, furthermore, death may take place without external cause.

If cells of the blood-red alga, previously mentioned as allied to the red-snow, are collected from hollows in stones, casually full of rain-water, and are kept dry for weeks and then again moistened, the water is found to have a very powerful effect. The protoplasm becomes mobile, and swarm-spores are formed which put forth vibratile cilia, propel themselves about for a short time in the water, and then settle down in some favoured spot, draw in their cilia, come to rest and divide, producing offspring which again are motile. This alga may be kept dry for months, nay even over a year, and still its cells exhibit the movements above described when put into water. But if a mass of it is preserved under these same conditions for many years and then moistened, the little cells will, it is true, take up additional water, but motile cells are no longer formed. The cells do not move, nor grow, nor divide, but gradually become discoloured; are first disintegrated and then dissolved. We say then that in them life could no longer be recalled, and we describe them as dead.

The same thing is observed in great cell-communities. The seeds of many species of plants preserve the capacity for germination for an incredibly long period, especially when kept in a dry place. If after ten years such seeds are transferred into

moist earth, the protoplasm in the majority of cases begins to bestir itself and to move, and the embryo grows out into a seedling. After twenty years, perhaps, only about five per cent of the seeds preserved would germinate. The rest are not stimulated by damp earth to further development; their protoplasm no longer possesses the power of augmenting its volume by absorption of matter from the environment, or of developing a definite form, but is disintegrated by the influx of air and water and breaks up into simpler compounds. After thirty years hardly one of the seeds would sprout. Yet all these seeds were kept throughout the time at one place and under precisely the same external conditions; nor can the slightest change in their appearance be detected. Gardeners express the fact by saying that the capacity for germination becomes extinct in from twenty to thirty years. But what kind of a force is this which may perish without a physical change of the substance concerned affording the basis of the extinction? In former times a special force was assumed, the force of life. More recently, when many phenomena of plant life had been successfully reduced to simple chemical and mechanical processes, this vital force was derided and effaced from the list of natural agencies. But by what name shall we now designate that force in nature which is liable to perish whilst the protoplasm suffers no physical alteration and in the absence of any extrinsic cause; and which yet, so long as it is not extinct, causes the protoplasm to move, to inclose itself, to assimilate certain kinds of fresh matter coming within the sphere of its activity and to reject others, and which, when in full action, makes the protoplasm adapt its movements under external stimulation to existing conditions in the manner which is most expedient?

This force in nature is not electricity nor magnetism; it is not identical with any other natural force, for it manifests a series of characteristic effects which differ from those of all other forms of energy. Therefore, I do not hesitate again to designate as vital force this natural agency, not to be identified with any other, whose immediate instrument is the protoplasm, and whose peculiar effects we call life. The atoms and molecules of protoplasm only fulfil the functions which constitute life so long as they are swayed by this vital force. If its dominion ceases, they yield to the operations of other forces. The recognition of a special natural force of this kind is not inconsistent with the fact that living bodies may at the same time be subject to other natural forces. Many phenomena of plant life may, as has been already frequently remarked, be conceived as simple chemical and mechanical processes, without the introduction of a special vital force; but the effects of these other forces are observed in lifeless bodies as well, and indeed act upon them in a precisely similar manner, and this cannot be said of the force of life.

Were we to designate as instinctive those actions of the vital force which are manifested by movements purposely adapted in some manner advantageous to the whole organism, nothing could be urged against it. For what is instinct but an unconscious and purposeful action on the part of a living organism? Plants, then, possess instinct. We have instances of its operation in every swarm-spore

in search of the best place to settle in, and in every pollen-tube as it grows down through the entrance to an ovary and applies itself to one definite spot of an ovule, never failing in its object. The water-crowfoot, in deep water, fashions its leaves with finely divided tips, large air-passages, and no stomata; whilst, growing above the surface of the water, its leaves have broad lobes, contracted intercellular spaces and numerous stomata. *Linaria Cymbalaria* (see fig. 11) raises its flower-stalks from the stone wall over which it creeps towards the light, but as soon as fertilization has taken place, these same stalks, in that very place and amidst unchanged external conditions, curve in the opposite direction, so as

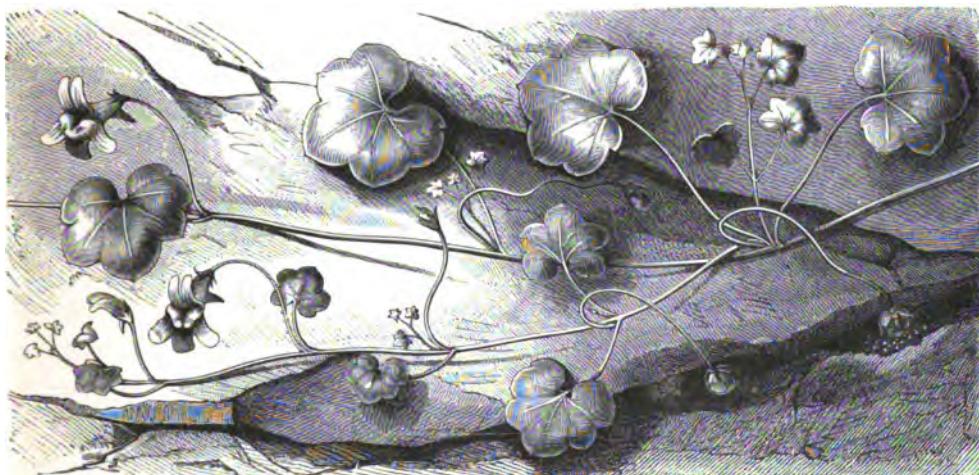


Fig. 11.—*Linaria Cymbalaria* dropping its Seeds into Clefts in the Rocks.

to deposit their seeds in a dark crevice. The flower-stalk of *Vallisneria* twists itself tightly into a screw and draws the flowers, which previously it had borne upon the surface of the water, down to the bottom when their stigmas have been covered with pollen-dust at the surface. These are all cases of unconscious action for a definite object, that is to say, they are the result of instinct.

If, however, we attribute instinct to living plants, it is but a step further to consider them as endowed with sensation also. Feeling in animals is the concomitant of a condition of disturbance in nerves and brain caused by a stimulus, which acts on the organs of sense, and is conveyed by nerves to the central organ. The transmission of the stimulus and the excited state of the brain and nerves are only molecular movements of the nervous substance, or, let us say, of the protoplasm, for nerve-fibres and nerve-cells are simply protoplasm developed in a particular manner. But the state induced by the stimulation of protoplasm, which is what we call sensation, cannot be essentially different in vegetable protoplasm from what it is in animal protoplasm, since the protoplasm itself, the physical basis of life in both plant and animal, is not different. In isolated plant-cells, indeed, it may amount to such a concentration of the condition of stimulation as to be called sensation, for the cell-nucleus is to all appearance

a central organ in relation to the protoplast that lives in a solitary cell. It is not of course to be supposed that within a whole plant-structure, that is in the community of live protoplasts which constitutes an individual plant, such a concentration of stimulation could occur as is the case with individual animals which have nerve-fibres all converging into the brain; but between the sensation of animals without nerves and that of plants no essential difference can exist.

Hence we infer that there is no barrier between plants and animals. The attempt to establish a boundary-line where the realm of plants ceases and the animal world begins is a vain one. If we naturalists, all the same, agree to separate plants and animals, we do so only because experience shows that a division of labour conduces to a speedier attainment of our object. On the intermediate ground where animals and plants meet, zoologists and botanists encounter one another, not, however, as hostile rivals with a view to exclusive possession of the field, but as colleagues with a common interest in the administration and cultivation of this jointly tenanted region.

# ABSORPTION OF NUTRIMENT.

---

## 1. INTRODUCTION.

Classification of plants with reference to nutrition.—Theory of food-absorption.

### CLASSIFICATION OF PLANTS WITH REFERENCE TO NUTRITION.

The object of a plant's vital energy, next in importance to the resistance of such influences as are likely to bring about the death of the protoplasm, is growth, *i.e.* the addition of substance to its body, or, in other words, the absorption of nutriment. A living plant, whether consisting of a single cell or of a vast community of cells, takes up food from its environment in quantities varying according to the needs of the moment. But its method of action—how it sets about acquiring possession of this raw material, how it manages to incorporate the substances absorbed from without, how it contrives to retain only such part as is useful to it, and to reject and get rid of, like ballast, what does not subserve its own growth—is infinitely varied. This variety in the processes of food-absorption corresponds, on the one hand, to differences in the habitat of plants, and, on the other, to the requirements of particular species, which requirements in their turn depend upon a specific constitution of the protoplasm in each species concerned. The difference must be very great between this process as manifested in plants which are immersed in water during their whole lives and the same as it occurs in plants which live in desert sands and are not supplied with water for months together. And again, absorption in those fungi which grow luxuriantly on damp timber in the deep obscurity of a mine must take place very differently from the corresponding process in the delicate alpine plants which on our mountain slopes are exposed periodically to the most intense sunlight, and then, for weeks at a time, are wreathed in sombre mists. So, also, the reciprocal action between plants and their environment must have a character of its own in the case of parasitic growths which absorb their food from other living organisms, and in those remarkable plants, too, which catch and devour small insects, and in such minute organisms as yeast, the vinegar ferment, and others, which play so important a part in our daily life, and lastly, in the gigantic trees which form our forests.

To acquire a general notion of these forms, with reference to their varieties as regards nutrition, it is best to classify them in the first place in groups according to their habitat, viz.: into water-plants or hydrophytes, stone-plants or lithophytes, land-plants, and epiphytes. But here again it is necessary to remark that no sharp

line of demarcation exists between these groups; all are connected by numerous intermediate links, and there are forms which belong to one group at one stage of development and to another at another stage.

The distinctive property of aquatic plants is that they derive their nourishment either entirely or principally from the surrounding water. Some preserve their freedom, floating or swimming about in the liquid medium; but the majority are fixed somewhere under the water by special organs of attachment. Many plants that are rooted in the mud at the bottom of pools are able to derive their food from the water when it is high, and when it is low, from the atmosphere as well: such amphibious organisms form a transitional group between water-plants and land-plants. The number of lithophytes is comparatively very small. They include those lichens and mosses which cling in immediate contact to the surface of stones and derive their food in a fluid state direct from the atmosphere. All lithophytes are so constituted that they can, without injury, dry up and suspend their vitality for a time when there is a failure of atmospheric precipitation lasting over a long period or when the air itself is very dry. But not every plant which grows upon rocks is to be regarded as a lithophyte in the narrower acceptation of the term. Those that are rooted in earth in the cracks and crevices of the rock must be classed amongst land-plants. To this class indeed more than half the plants now in existence belong. Though surrounded by air as regards a part of their structure they have another part sunk in the soil, and from the soil they take up water and inorganic compounds in aqueous solution. Plants which grow attached to other plants or to animals are called epiphytes.

The majority of plants are during the period of food-absorption connected with the foster-earth and are not capable of locomotion. The plant being fixed to one spot must therefore sooner or later exhaust the ground in its neighbourhood, and must require a further supply of nutritive substances. The parts specially devoted to food-absorption often lengthen out in these circumstances beyond the impoverished region, and thus endeavour to bring areas more and more distant within the range of absorption. Many plants possess the faculty, to which reference has already been made, of alluring animals and of killing and sucking their juices. Not only amongst saprophytes and parasites, but also amongst aquatic plants, instances occur in which certain movements are performed involving the whole body of the organism, with a view to promoting the absorption of nutriment. Particularly striking in this respect are many plasmoid fungi (which we may well refer to here, not on this account alone, but also for the additional reason that they take in nourishment without the intervention of a cell-membrane). The naked protoplasm in these cases, which include in particular the class of Amœbæ, crawls in its search for food over the nourishing substratum, and derives from it immediately the materials needful for growth. Loose bodies are liable to be seized by the radiating processes of the protoplasm, which then closes round them and drains them completely of their juices (see fig. 9, the last figure to the right). These bodies encompassed by the protoplasm, if small, are drawn inwards from the periphery and are regularly digested in the

interior. Such parts of foreign bodies as are not serviceable for nutrition are subsequently eliminated or are left behind by the protoplast as it creeps onward. But this method of food-absorption is limited to amœboid forms belonging to the boundary-land of animal and vegetable life. The movements of other naked protoplasts, such as those which are carried about in the water by vibratile cilia, have nothing to do with the search for food or with its absorption, but are connected rather with the processes of distribution and propagation.

#### THEORY OF FOOD-ABSORPTION.

In the case of protoplasts inclosed in cell-membranes the food necessary for nourishment must always pass through the cell-membrane and peripheral protoplasmic layer (ectoplasm) into the interior of the protoplasmic bodies. And so, conversely, such of the substances absorbed as are of no use in the construction of the organism or for any other purpose, must be separated and passed out through these envelopes. The cell-membranes of those protoplasts which are employed in absorbing food must accordingly have a special structure: the ultimate particles must be so arranged as to allow of the passage of nutritious material inwards, and of rejected matter outwards, without prejudice to their own stability. The passages in cell-walls used for this purpose are very minute, much smaller at all events than the pore-canals described above as being occupied by fine protoplasmic filaments; the dimensions are in fact so trifling as to be invisible even with the best microscopes. Still we are forced to conclude that they exist by *a posteriori* reasoning from a series of phenomena, and to assume that the cell-membrane, like almost every other kind of body, consists not of continuous matter, but of minute particles, which are termed atoms, and are separated from one another by infinitesimally small spaces. Various processes and appearances have also led physicists and chemists to the conclusion that these atoms are not aggregated in disorder, but are always combined together in groups of two or more, even in the case where all the atoms in a body are of the same kind, *i.e.* are the same element. If a body contains different elements they are not mixed together indiscriminately, but are grouped in conformity to a definite law: every group includes atoms of all the different elements concerned, arranged in a certain invariable manner, not only as regards number, but also as regards relative position. Groups of atoms of this kind are called "molecules," and the spaces between them are supposed to be larger than those between single atoms. Further, it is not improbable that the molecules themselves form groups, each group consisting of molecules conglomerated in a definite manner, and that the passages separating these molecular groups are larger again than those separating the single molecules within each group. These groups of molecules have been called "micellæ" or Tagmata, and they also are supposed to be aggregated together in definite order.

According to this theory the cell-membrane is analogous to a sieve, the pores of which are grouped in a definite manner, the broadest perforations being between

the micellæ or groups of molecules, narrower apertures between the molecules or groups of atoms in each micelle, and lastly the finest pores between the atoms themselves in each molecule. These interspaces are liable to contraction and expansion, for the union of the molecules is affected by two forces, one of which manifests itself as a mutual attraction between atoms and atomic groups, whilst the other tends to drive atoms and molecules asunder. Of these forces the former, i.e. the attractive force existing in all material particles, is called chemical affinity when it causes atoms of different kinds to unite to form a molecule; and it is called cohesion when applied to the mutual attraction of similar molecules, and adhesion where it holds together masses of molecular groups with their surfaces in contact. The action of heat is opposed to this attractive force, which is only effective at infinitesimal distances. Bodies are all caused to expand by heat, their atoms, molecules, and micellæ being forced apart. Heat is believed to be a vibratory motion of these ultimate particles, and it is supposed that the greater the vibrations the greater is the separation of atoms and atomic groups, the interspaces expanding and the heated body increasing consequently in volume. As is well known, the atoms and molecules may be forced so far apart by increase of temperature that cohesion is entirely overcome, and solids are converted, first into liquids and at last into gases.

The interspaces or passages between the molecules and molecular groups composing a cell-membrane are penetrable by molecules of other substances, provided always, firstly, that the admitted molecules are not larger than the passages; and secondly, that there exists between the molecules of the cell-wall and those of the penetrating body that sort of attractive force which has been designated chemical affinity. Both premises are satisfied in the case of aqueous molecules, and experiment proves that they are admitted into the inter-molecular spaces of a cell-membrane with great ease and readiness. The cell-membrane saturates itself with water, or, to use the technical phrase, it has the tendency and ability to "imbibe" water. The force of attraction between molecules of a cell-membrane and water-molecules is indeed so intense that the cohesion of the molecules in the membrane is partially neutralized, and the imbibed water causes them to move apart. In consequence of this, the cell-membrane swells up and its dimensions are increased.

It is also supposed that the micellæ of a cell-membrane attract and admit water-molecules to such an extent as to surround themselves with watery envelopes. Such a condition would no doubt be nothing but beneficial, promoting, as it would, the interchange of materials through the cell-membrane, and the mixing of fluid substances situated on either side of the porous membrane. At all events this mixing process must ensue in the interspaces of the cell-membrane; and, in the particular case out of which this discussion has arisen, viz. food-absorption, the interacting substances are, on the one hand, the compounds in the soil outside the cell-membrane, and, on the other, the organic compounds under the control of the live protoplast within the cell-membrane. Both the outgoing and the incoming substances must be soluble in water, and must, therefore, have an attraction

for water. But the power of a substance in aqueous solution, whether without or within the cell-membrane, to permeate the saturated pores, and to mix thoroughly there, certainly depends also on the degree of chemical affinity and of adhesion existing between the molecules and micellæ of the cell-membrane on the one hand, and these infiltrating substances on the other. A very complex interaction of forces takes place which we cannot here investigate any further, as it would take us much too far afield.

Returning to the explanation of food-absorption, attention must be drawn to the fact that the mixing or diffusion which takes place through the cell-membrane differs from the free diffusion which would occur if the cell-membrane were not present. Experiment has proved that if one side of a cell-membrane is steeped in a saline solution and the other in an equal volume of pure water, the number of saline particles which pass through into the water are many fewer than the number of water-particles which pass into the solution of salt; and, moreover, if an organic compound, such as albumen or dextrin, is on one side, and water on the other, water transfuses to the organic compound, whereas no trace of the albumen or dextrin (as the case may be) passes through to the water. Now this phenomenon, which is called "osmosis" ("endosmosis and exosmosis"), is of great importance for the conception we have to form of food-absorption. It is clear that, whilst water and substances dissolved in water are brought under the control of the protoplast within a cell through the cell-membrane, as a consequence of the action of albuminous and other compounds constituting the body of the protoplast, and of the salts dissolved in the so-called cell-sap in the vacuoles, there is no necessity for any part of the cell-content to pass out through the cell-membrane. Thus the protoplasm is able to exercise an absorptive action on aqueous solutions outside the cell-membrane, and to continue to absorb until the cell is filled. Indeed, the chemical affinity for water possessed by the substances in a cell may occasion so great an absorption of water that, in consequence, the volume of the cell is enlarged and the cell-membrane is subjected to pressure from within. The cell-membrane is able to yield to this pressure to the extent permitted by its elasticity; but excessive stretching of the cell-membrane is at length counteracted by cohesion, and thus a condition is attained in which the cell-contents and the cell-membrane are subjected to mutual pressure, a state which is called "turgidity."

The process just described, of the absorption of water in large quantities into the precincts of the protoplasm without any simultaneous transmission of matter to the outside, is certainly in no respect an exchange. But it obviously does not exclude the possibility of a real exchange taking place between substances on either side of a cell-membrane, *i.e.* between solutions in the soil and those in the cell-sap contained in lacunæ of the protoplasm. Certain phenomena in fact put it beyond doubt that on occasion a real exchange of this kind does occur. But it is complicated by the circumstance that substances in process of being exchanged have to pass not only through the cell-membrane but also through the primordial utricle; and the primordial utricle consists of molecules of a kind other than

those of the cell-wall, having different chemical affinities, and these molecules again are differently grouped; nor are the passages for aqueous solutions the same. All this cannot but have an important bearing on the permeating capacity of the substances that are being interchanged.

Although all these ideas concerning the molecular structure of cell-membranes and of protoplasm, concerning the intermixture and exchange of materials and the absorption on the part of cells and their swelling up, have only the value of theories, still we have good ground for assuming that they are fairly near the truth. They give us, at all events, an intelligible representation of the interaction which takes place between living protoplasts, with their need for food, and the environment, which supplies the nutriment.

---

## 2. ABSORPTION OF INORGANIC SUBSTANCES.

**Nutrient Gases.—Nutrient Salts.—Absorption of Nutrient Salts by Water-plants, Stone-plants, and Land-plants.—Relations between the position of Foliage-leaves and Absorption-roots.**

### NUTRIENT GASES.

One of the most important sources of the nourishment of plants is carbonic acid. The living protoplasts appropriate it from water and from air, in the latter case chiefly by attracting the carbon-dioxide.<sup>1</sup> This gas penetrates a cell-wall saturated with water more readily than the other constituent gases of the atmosphere (nitrogen and oxygen). In the wall it is converted into carbonic acid, and it then passes on into the cell-sap contained in the cavities of the protoplast. Apart from the effects of temperature and atmospheric pressure, the quantity of carbonic acid absorbed is chiefly determined by the requirements of the cells whose nourishment is in question. These requirements, however, vary considerably according to the specific constitution of the protoplasm and with the time of day. During daylight the need of carbon is very great in all green plants. As soon as the carbonic acid reaches the cell-sap it is decomposed and reduced by the action of sunlight, and from it are formed compounds known as carbo-hydrates. The oxygen thus set free is, however, removed from the cell precincts, and expelled into the surrounding air or water. In this way the gas when barely absorbed is withdrawn, as such, from the cell-sap, the carbon alone being retained and the oxygen eliminated, and a renewed attraction of carbon-dioxide from the surrounding medium ensues. The fresh supply again is immediately worked up in the green chlorophyll-bodies, so that there is a constant influx of carbon-dioxide, and therefore indirectly of carbonic acid, from the environment into the interior of green cells to the part where its consumption takes place. Were it possible to see

<sup>1</sup> The atmosphere contains free carbon-dioxide and not carbonic acid. But carbonic acid is formed when the dioxide is absorbed into water.

the molecules of carbon-dioxide in the air, we should observe how much faster they are impelled towards the leaves and other green parts of plants, where the intense craving for carbon is localized, than are the other constituent particles of the air. This impulsion and influx lasts so long as the green cells are under the influence of daylight. The first thing in the morning when the first ray of sunshine falls upon a plant the protoplasts begin work in their little laboratories decomposing carbonic acid, and producing from it sugar, starch, and other similar organic compounds. And it is not till the sun sets that this work is suspended, and the influx of carbon-dioxide stopped till the following morning.

The green plants that spend all their lives under water are supplied with carbonic acid by the water surrounding their cells, which always contains some of that material. In the case of unicellular plants of this class, absorption of carbonic acid takes place through the whole surface of the cell-membrane. Multicellular plants, with their cells arranged in filaments or plates, only take in carbonic acid through those parts of the walls of their cells which are in immediate contact with the water. This applies also to submerged plants composed of several layers of cells and of considerable dimensions. Thus, in plants of this kind, the cells in contact with the water constitute the skin. They are always pressed closely together and squeezed flat, are not thickened on the side exposed to the water, and are united everywhere edge to edge leaving no gaps. But in the interior of these water-plants large lacunæ and cavities are formed from earliest youth, owing to the detachment of single rows of cells; and the spaces so formed are filled with a quantity of nitrogen, oxygen, and carbon-dioxide, that is to say, with a gaseous mixture not essentially different from atmospheric air. Although this organization may have as its primary object the reduction of the plant's weight as a whole, it cannot be without a further importance inasmuch as carbonic acid can be taken up from the air-spaces into adjacent cells. But there is no doubt that, even in this case (of water-plants provided with large internal air-cavities), the chief absorption of carbonic acid is through the epidermis, or more precisely through those walls of the epidermal cells which are in immediate contact with the water.

The carbonic acid taken up by cells, wholly or partially immersed in water, is either contained as such dissolved in the watery medium, or occurs in combination with calcium as bicarbonate of lime. Part of the carbonic acid in this bicarbonate in aqueous solution is susceptible of being withdrawn by water-plants, mono-carbonate of lime, which is insoluble in water, being then precipitated on the cell-wall through which the rest of the carbonic acid has passed into the cell-interior. Accordingly, a large number of water-plants are found incrusted with lime in both fresh and salt water. We shall return to this important phenomenon when we treat of the influence of living plants on that part of the environment which comes within their sphere of action for purposes of nutrition.

Lithophytes obtain carbonic acid from the moisture deposited upon them from the aqueous vapour in the atmosphere, and attract carbon-dioxide direct from the

air around them. The chief members of this class are those mosses, liverworts, and lichens which, though clinging to dry rocks, behave just like water-plants as regards the absorption of carbonic acid. There is no reason to think that these plants absorb carbonic acid in dry weather; for under the influence of dry air they lose water fast, and meanwhile receive no compensation from the rock to which they are attached, and in a short time they become so dry that they crumble into powder when rubbed between the fingers. Vitality is suspended for a time, and it is out of the question that there should be any absorption of carbon-dioxide from the atmosphere under such circumstances. But the moment the plant is moistened by rain or dew, the cell-walls directly exposed to the air become saturated, and are enabled to admit water into the interior. Then the lithophytes suck up water very fast; the dry, apparently dead, incrustations swell up again, and, together with the rain and dew, carbonic acid is absorbed, it being contained in all depositions of atmospheric moisture. A tumescent moss tuft can, in addition, absorb carbon-dioxide direct from the atmosphere through its saturated superficial cells; but the quantity of carbonic acid thus acquired by a plant is in any case only secondary. Many mosses, as for example the widely-distributed *Grimmia apocarpa*, are also able to live just as well under water as in air; nor is any alteration of their leaves necessary in either condition, nor any special contrivance for the absorption of carbonic acid and water. These substances reach the interior by similar passage through cell-walls of identical construction, whether the *Grimmia* spends its life attached to submerged rocks or in the open air at the top of a mountain; whence we may infer that there is a greater resemblance between lithophytes and water-plants as regards nutrition than between lithophytes and land-plants.

Land-plants satisfy their need of carbon almost exclusively by withdrawing the dioxide from atmospheric air. For the purpose of this direct appropriation, specially adapted structures are found in them. Seeing that these plants are not able to endure periodic dessication in times of drought, as lithophytes are, it is necessary for them to be secured against excessive loss of water. Accordingly, the cell-walls in immediate contact with the air, that is to say, the outer walls of the epidermis, are thickened by a layer (cuticle) which is impermeable by air or water, and, in general, they are so organized that water cannot readily escape from the interior of the cells. Obviously, however, a cell-wall which opposes a strong resistance to the extravasation of water will not give easy admittance to an influx either, and the conditions for the passage of gases through a cell-membrane, thickened and cuticularized in this way, would be far from favourable. As a matter of fact many of the constituent gases of the atmosphere permeate these thickened walls of the epidermal cells only with great difficulty, and others not at all. Carbon-dioxide alone has the power of penetrating, but even in the case of this gas the quantity is not always sufficient to satisfy the demand. To ensure that so important a form of plant-food should reach in proper amount those cells lying under the epidermis, which are occupied by protoplasts engaged in the regu-

lation of nutrition, there is an adaptation of structure of the following nature. Among the firmly connected epidermal cells with their thickened outer walls almost impervious to air, other cells are interspersed at intervals. They are always in pairs, are generally rather smaller than the rest, and have a little cleft open between them. Inasmuch as these apertures (stomata) always exist where passages and canals, the so-called intercellular spaces, have arisen from the separation of individual cells of the sub-epidermal tissues, each stoma constitutes the mouth of a system of channels ramifying between the thin-walled cells of the interior. The components of the atmosphere, especially carbon-dioxide, are able to reach these internal passages through the stomata, and in them they travel to the chlorophyll-containing cells. Through the thin, saturated walls of these cells they are able to penetrate with ease, and so they reach the living protoplasts, with their equipment of chlorophyll, whose daily work it is, as already mentioned, to decompose—under the transforming power of light—the carbonic acid as it reaches the chlorophyll-bodies, to work up the carbon and expel by the same path as they entered not only the oxygen but also all other aerial constituents which may have penetrated and for the moment find no employment.

These ventilation-canals, with stomata as orifices at the epidermis, have other uses besides the importation of carbon-dioxide (and therefore of carbonic acid) and the exportation of oxygen. For the same pores, passages, and lacunæ, as serve for the influx and exit of carbon-dioxide and oxygen respectively, are the channels of a plant's respiration. Moreover, they play a very important part also in the escape of aqueous vapour, the process known as "transpiration;" and as the variety in their structure is to be interpreted chiefly as an adaptation to the different conditions under which transpiration occurs, it cannot be profitably discussed until we treat of that process.

Those saprophytes and parasites which contain no chlorophyll or practically none, do not absorb any free carbon-dioxide from the atmosphere, but supply themselves with carbon from the organic compounds in the nutrient substratum on which they grow. But saprophytes and parasites, abundantly furnished with chlorophyll, doubtless do attract free carbon-dioxide in addition. They may do so either after the manner of water-plants and lithophytes, as is the case with Euglenæ, and with mosses growing on the dung of mammalia; or else after the manner of land-plants, as instances of which the cow-wheat, yellow-rattle, and eye-bright may be quoted.

It is a very remarkable fact that no plant is known which takes up carbon-dioxide or carbonic acid from the earth. One might expect that the roots of land-plants at any rate, ramifying as they do in a stratum of earth saturated with water containing carbonic acid in solution, would suck up to some extent so important a food, and that it would be from them conducted to the green-foliage leaves. But so far as experiments have gone, they indicate that this is not the case.

Equally curious is the circumstance that nitrogen, which is an indispensable constituent of protoplasm, and therefore a very important means of subsistence, is

not absorbed from the surrounding air, although, as is well known, the atmosphere contains nitrogen to the amount of 79 per cent of its volume. There can be no doubt that though nitrogen permeates the cell-walls of an air-encompassed plant much less readily and quickly than carbon-dioxide, yet it is carried from the atmosphere into the ventilation-spaces of green foliage-leaves, and further through the thin cell-walls into the laboratories of the protoplasts, where one would expect it to be worked up in the same way as carbonic acid. The most careful experiments have determined, however, that it is not turned to account in this form by the protoplasts, but that on the contrary it is given back unused to the air, and only such nitrogen as reaches the interior of plants in combination with other substances is of any service there.

The principal sources of the nitrogen required by plants are nitrates and ammoniacal compounds absorbed from the ground; but nitric acid and ammonia themselves, of which there are traces in the atmosphere and in water, must not be overlooked. The quantity of nitric acid in air is, it is true, even less than that of carbon-dioxide; but just as the small amount of carbon-dioxide can be absorbed from the air with highly productive results, so may also the still smaller proportion of nitric acid be turned to account. The sources of nitric acid are dead organic bodies as they decompose and become oxidized. In many ways the process of formation of nitric acid from decaying bodies may take place so as to produce ammonia in the first place and from it nitric acid. It would seem possible, though it is an unproved assumption, that in places where dead bodies of plants and animals, vegetable mould, manure, and such things are undergoing oxidation, that is to say, in woods and fields, the small quantities of nitric acid that are given off are immediately taken up by the plants growing there. It must be borne in mind that plants behave with reference to what is necessary or useful to them like a chancellor of the exchequer preparing his budget; they take these things where they find them.

The question has been raised, too, as to the source from which the first plants that appeared on the earth were able to obtain nitric acid. We are obliged to assume that, at that time before the existence of nitrogenous organisms to supply nitric acid by oxidation of their dead bodies, all nitric acid, and therefore all the nitrogen used in the nourishment of plants, was generated by thunder-storms. We know that nitric acid is formed in the air on occasion of electric discharges and is deposited on the earth together with rain and dew. This source of nitric acid is not yet exhausted, and even at the present day it no doubt plays the same part as in the ages long past at the commencement of all vegetable life.

If nitric acid is used by protoplasts, in the building up of the highly important albuminous compounds, it is broken up in a manner similar to the decomposition of carbonic acid to form carbohydrates, that is to say, oxygen is separated out. In this case, however, sunlight and, therefore, chlorophyll are not immediately concerned. Moreover, the oxygen that is set free is not eliminated, but is used in the manufacture of other compounds in process of formation in the plant, probably in that of vegetable acids.

Ammonia behaves in relation to plants just in the same way as carbon-dioxide and nitric acid. It is disengaged from dead decomposing organic bodies, and is found in traces, either alone or with equally minute quantities of carbon-dioxide and carbonic and nitric acids in the air, in atmospheric deposits, and in all water wherein animals and plants reproduce their kind, the old individuals dying and making way for the young. Water-plants are all limited to this source for acquisition of nitrogen. As regard lithophytes, it stands to reason that they must derive their nitrogen from the ammonia contained in the air, in atmospheric deposits, and from nitric acid. Whence otherwise could a crustaceous lichen attached to a quartz rock on a mountain supply itself with the nitrogen essential for the growth of its protoplasm? Moreover, some of the larger lithophytes, especially mosses, seem to be capable of absorbing ammonia direct from the air. An observation made in the Tyrolese Alps has some bearing on this question:—The ridges of the Hammerspitze, a peak rising to 2600 meters between the Stubaithal and the Gschnitzthal, is, in favourable weather in the summer, the resting-place of hundreds of sheep, and is consequently covered with an entire crust of the excrements of these animals. A highly offensive and pungent smell of ammonia is evolved, and renders a prolonged stay on this spot anything but pleasant, notwithstanding the beauty of the view. Now, it is worthy of note that the mosses, which are produced in abundance on the rocks above this richly-manured ground, but are not themselves actually amongst the sheep-droppings, exhibit a luxuriance unparalleled on any of the neighbouring summits belonging to the same formation but unfrequented by sheep. The gaily-coloured green carpet extends as far as the ammoniacal odour is perceptible, and it is natural to suppose that this luxuriant growth is stimulated by the absorption of ammonia direct from the air.

Land-plants also can take up ammonia from the air. It has been shown that the glandular hairs of many plants, for instance those on the leaves of *Pelargonium* and of the Chinese Primrose, have the power of absorbing traces of ammonia, and of sucking up carbonate and nitrate of ammonia in water with rapidity. When we consider that a single one of these primroses (*Primula sinensis*) possesses two and a half millions of absorbent glandular hairs so placed as to be able to take up the ammonia brought to the plant by rain, we are unable to look upon this process as of altogether trifling importance. It is highly probable that almost all ammonia, after its formation from decaying substances in the ground, is at once absorbed by the plants growing in the immediate neighbourhood, and that the relatively small quantity of ammonia in the upper atmospheric strata is referrible to this cause. The splendid luxuriance of the pelargoniums, thickly studded with glandular hairs, which one sees in front of cottage windows in mountain villages where a dung heap is close by, and in the windows of stables, frequently excites admiration and surprise. Whether it is due to the fact that in these situations there is the possibility of absorbing an unusually large quantity of ammonia is a question which we will leave undecided.

## NUTRIENT SALTS.

If wood, leaves, seeds, or any other parts of plants are subjected to a high temperature with free access of air, the first changes that occur are in the compounds of nitrogen and of carbon contained in the heated matter. They turn black, are charred and burnt, and ultimately the products of combustion pass into the atmosphere in gaseous condition. The incombustible part which remains behind is called the "ash." The quantity of this ash, as well as its composition, varies very much in different species of plants, and even in different parts of the same plant. Generally the weight of ash is only one or two per cent of the entire weight of the plant in a dry state before burning. The greatest relative proportion of ash is that which is obtained from the combustion of those hydrophytes which live in the sea; and next in quantity is the ash of the family of Oraches which abound on salt-steppes. On the other hand, the smallest quantity is that afforded by fungi and mosses, by *Sphagnum* in particular, and with these must be mentioned the tropical orchids living on the barks of trees. Seeds and wood yield relatively much less ash than leaves. But, as above remarked, some ash is formed upon the combustion of any part of a plant or even of a single cell, and this residue of ash sometimes allows of our recognizing exactly the size, form, and outline of the cells. The universal distribution of ash-forming constituents permits us to conclude with certainty that they do not exist fortuitously in plants, but are essential to them. That these constituents are indispensable may also be proved directly. If an attempt is made to nourish a plant on filtered air and distilled water exclusively, the plant soon dies; but if a small quantity of the constituents of its ash are added to the distilled water in which the roots are immersed, the plant grows visibly in the solution, and develops leaves and flowers and even seeds capable of germination.

Experiments of this kind with cultures have been the means of almost completely establishing the division between those constituents which are indispensable for all plants, and those which are only necessary under certain conditions and to particular species, or, still less, only beneficial. Those elements must be regarded as essential, which are used by plants for the process of construction, and enter into the composition of the protoplasm or of the cell-membrane—such, for instance as are essential constituents of proteid substances, or are in some way necessary to the formation of these products. Amongst these must be included sulphur, phosphorus, potassium, calcium, and magnesium. Some plants, especially those that live in the sea, require sodium, iodine and chlorine, and, for green plants, iron is necessary. Silicon is also very important for most plants in helping them to flourish in the wild state. Most of these elements are taken into a plant, in the course of nutrition, in a condition of extreme oxidation, that is to say in combination with a quantity of oxygen; in fact, as a general rule, they are absorbed in the form of salts, and we may for the sake of brevity include all the mineral food-stuffs under the name of nutrient salts or food-salts.

It is obvious that food-salts can only pass through cell-membranes and reach the interior of a plant in a state of solution. On this account the soluble sulphates, phosphates, nitrates and chlorides of calcium, magnesium, potassium and iron, may pre-eminently be called food-salts. Whether an essential element is absorbed by a plant in the form of one of these compounds or another appears to be unimportant; phosphorus, for example, may be proffered by the soil in the form either of potassium phosphate or of sodium phosphate, with like results. As regards the importance of sulphur to plants, it is at any rate established that it is necessary for the production of proteid substances. Phosphorus appears to be indispensable in the transformation of certain compounds of nitrogen. Potassium is supposed to play a part in the formation of starch. Calcium is introduced into plants in combination with sulphuric acid as calcium sulphate. This salt is decomposed, the lime combining with oxalic acid to form insoluble calcium oxalate, and the sulphur going to form the sulphuric acid which is used in the construction of albuminous substances or proteids. Lime is therefore important, inasmuch as it is a medium of transport for sulphur. Iron certainly participates in the formation of chlorophyll, even if it does not enter into its composition, as was formerly supposed. For, it has been proved, by means of artificial cultures, that plants reared in solutions free from iron were white instead of green, and died at last; whereas, after the addition of a small quantity of a soluble iron salt, such plants became green in a very short time, and were able to continue their development. The utility of most of these elements does not therefore appear to consist necessarily in their entering into the composition of organic compounds, but in the promotion and regulation of the constructive and destructive chemical processes.

Silicic acid, which occurs so plentifully in the ash of many plants as to constitute often more than 50 per cent, has a different function. If the minute unicellular water-plants known as Diatoms are incinerated, or if stems of Equisetum, Juniper-needles, or leaves of grasses, &c., are subjected to a red heat, white skeletons remain behind which consist almost entirely of silicic acid, and exhibit not only the forms of the cells, but even the finest sculpturing of the cell-walls. In particular, the stiff hairs on the leaves of grasses are preserved, and better still the cell-membranes of diatoms. The latter present very beautiful forms with their outlines quite distinct, and many structural properties of the cell-membranes, especially their moulding, striation, and the dots and other excrescences are to be seen much more clearly after than before ignition, when the transparency was less owing to the protoplasm occupying the interior of each cell. In order to describe exactly the very varied form of Diatomaceæ, specimens are carefully and thoroughly ignited, and the descriptions and illustrations of these microscopic plants are for the most part made from siliceous skeletons prepared in this way. These skeletons show clearly that silicic acid occurs only in the cell-membrane, and plays no part as constituent of any chemical compound in the protoplasm; nor does it appear to be instrumental in the formation of any such compound. The molecules of silicic acid are so closely packed and so evenly distributed amongst the mole-

cules of cellulose that, even after the removal of the latter, the entire structure is preserved in outline and in detail. They form, therefore, a regular coat of mail which may be looked upon as a means of protection against certain injurious external influences.

For a large number of plants living in the sea, sodium, iodine, and bromine also are of especial importance as food-stuffs. How far fluorine, manganese, lithium, and various other metals, which have been detected in the ash of some plants, are of use is not determined, for our knowledge is particularly incomplete with respect to the various uses subserved in nutrition and growth by the different mineral food-stuffs. It is worthy of note that alumina, which is so widely distributed and easily accessible to plants, is only very rarely absorbed. The ash of *Lycopodium* is the only kind in which this substance has been identified with certainty in any considerable quantities.

Lastly, amongst the sources of elements contained in the food-salts, we must consider the solid crust of the earth. But it is only in the case of comparatively few vegetable organisms that this earth-crust forms the immediate foster-soil. The majority derive the salts that nourish them from the products of the weathering of rocks, from refuse and the decaying remains of dead animals and plants, which, in decomposing, give back their mineral substances to the ground, from underground waters that filter through fissures in rocks and through the interstices of sandy or clayey soils soaking with lye, the adjacent parts of the earth's crust, and, lastly, from the water of springs, streams, ponds, and lakes, which have come to the surface holding salts in solution, as also from sea-water with its rich supply of salts.

The very salts that are needed by most plants are amongst the most widely distributed on the earth's surface. The sulphates of calcium and of magnesium, for example, and salts of iron, potassium, &c., are found almost everywhere in the earth, and in water, whether subterranean or superficial. At the same time it is very striking that these mineral food-salts are not introduced into plants by any means in proportion to the quantity in which they are contained in the soil, but that, on the contrary, plants possess the power of selecting from the abundance of provisions at their disposal only those that are good for them and in such quantity as is serviceable. This selective capacity of plants is manifested in many ways, and we will now briefly consider some of the most important of them.

In the first place we have the fact that plants reared close together in the same soil or medium may yet exhibit an altogether different composition of ash. This is particularly striking in water and bog-plants, which, though rooted in close proximity and immersed in the same water, show very considerable differences in respect of mineral food absorbed. The result, for instance, of testing specimens of the Water-soldier (*Stratiotes aloides*), the White Water-lily (*Nymphaea alba*), a species of Stone-wort (*Chara fætida*), and the Reed (*Phragmites communis*), all growing close together in a swamp, was as follows as regarded the potash, soda, lime, and silicic acid, held by them respectively:—

	Water-soldier.	Water-lily.	Stone-wort.	Reed.
Potash,.....	30·82	14·4	0·2	8·6
Soda,.....	2·7	29·66	0·1	0·4
Lime,.....	10·7	18·9	54·8	5·9
Silicic Acid,.....	1·8	0·5	0·3	71·5

The other constituents of the ash of these plants, in particular iron oxide, magnesia, and phosphoric and sulphuric acids, exhibited less marked differences; but the inequality in the amounts of potash, soda, lime and silicic acid are so great, as only to be explicable on the assumption of a power of selection on the part of these plants. Various species of brown and red sea-weeds, which had been attached to the same rock and developed in the same sea-water, showed similar variations in the composition of their ash.

On the mountains of serpentine rock near Gurhof, in Lower Austria, specimens of *Biscutella laevigata* and *Dorycnium decumbens* were collected from plants growing together, and one above the other, upon a declivity which they clothed. Their roots, interlaced here and there, were fixed in the same ground, and drew nourishment from the same store. The following table gives the composition of the ash in these two species:—

	Biscutella laevigata.	Dorycnium decumbens.		Biscutella laevigata.	Dorycnium decumbens.
Potash,.....	9·6	16·7	Silicic Acid,.....	13·0	6·3
Lime, .....	14·7	20·9	Sulphur,.....	5·2	1·6
Magnesia,.....	28·0	19·6	Phosphorus,.....	15·9	22·3
Iron Oxide,.....	7·8	2·8	Carbonic Acid,.....	5·4	9·7

The differences here seem to be not so great as in the case of the water-plants previously given, but they are sufficient to prevent our regarding them as merely the result of chance.

If, on the other hand, we compare the composition of the ash of different specimens of the same species, which have been reared on similar soils, but at great distances from one another, the discrepancies are comparatively slight. Foliage from beech-trees growing on the limestone mountains near Regensburg yielded an ash practically identical with that obtained from leaves of beeches on the Bakonyer-Wald hills in Hungary. The ash of different individuals of a single species even exhibits the same constitution, in the main, when those individual plants have obtained their nutriment from soils differing greatly in chemical composition. Only in cases where the quantity of a substance in one soil is more abundant than in the other there is generally a greater or less amount of it to be found in the ash.

That under these circumstances certain substances may replace one another is not improbable. But such substitution must be confined to those nearly allied compounds whose molecules are capable of being used indifferently by the formative

protoplasm in construction, and in the storage of materials. The annexed table, which gives side by side analyses of the ash of branches of the Yew (*Taxus baccata*) with their leaves attached, illustrates the replacement of calcium by magnesium:—

	Ash from branches and leaves of the Yew from		
	Serpentine.	Limestone.	Gneiss.
Silicic Acid,.....	3·8	3·6	3·7
Sulphuric Acid,.....	1·9	1·6	1·9
Phosphoric Acid,.....	8·3	5·5	4·2
Iron Oxide,.....	2·1	1·7	0·6
Lime,.....	16·1	36·1	30·6
Magnesia,.....	22·7 { 38·8	5·1 } 41·2	5·7 } 36·3
Potash,.....	29·6	21·8	27·6
Carbonic Acid,.....	14·1	23·1	24·4
Traces of Manganese, Chlorine, &c.,.....	—	—	—
Totals,.....	99·6	98·5	98·7

The Yew occurs in Central Europe on very various mountain formations, chiefly on limestone, but not infrequently on gneiss, and occasionally on serpentine rocks. On comparing the quantities of calcium and of magnesium in the ash of yews, grown on lime and on gneiss respectively, with those yielded in the case of serpentine formation, we find that magnesia preponderates considerably in weight over lime in a yew from serpentine rocks (which are in the main a compound of magnesia and silicic acid), whilst the proportion between these two salts is reversed in a yew grown upon limestone. The obvious inference from the table is that, in plants from a serpentine ground, lime is to a great extent replaced by magnesia. This is further supported by the circumstance that if lime and magnesia are counted together the resulting numbers are very near one another, namely 41·2 per cent of the ash for limestone, 38·8 per cent for serpentine rock, and 36·3 per cent for gneiss.

But all these phenomena observed in connection with the selection of food-salts are not nearly so surprising as the fact that plants are also capable of singling out from an abundance of other matter particular substances, which are of importance to them, even from a soil containing them in barely perceptible quantities, and of concentrating them to a certain extent. As has been shown above, nearly a third of the ash of the white water-lily is composed of common salt. One might, therefore, suppose that the water in which water-lilies flourish contains a particularly large quantity of common salt. But nothing of the kind is the case. The bog water which bathed the stem and leaves of this specimen only contained 0·335 per cent of common salt, and the mud through which the roots straggled contained only 0·010 per cent.

No less astonishing is it to find Diatomaceæ, with cell-membranes, as above mentioned, sheathed in silicic acid, existing in water which contains no trace of silicic acid. Above the Arzler Alp, in the Solstein chain near Innsbruck, there is a spring of cold water which falls in little cascades between blocks of rock. The

water of this spring is hard, and it deposits lime at a little distance from the source. Exactly at the spot where it wells out of a fissure in the rock its bed is entirely filled by a dark-brown flocculent mass which consists of millions of cells of the beautiful *Odontidium hiemale*, a species of diatom with siliceous coating. These cells are ranged together in long rows, and are present in numbers and luxuriance such as are scarcely ever to be observed in other situations. Yet the spring water flowing round contains so little silicic acid that no trace of this substance could be discovered in the residue from the evaporation of 10 litres.

An instance similar to this of silicic acid, is afforded by the iodine in the sea. Most of the sea-wracks inhabiting the North Sea contain iodine, many indeed in considerable quantity, and yet we have not hitherto succeeded in detecting iodine in the water of the North Sea. Similar phenomena, sometimes quite baffling explanation, are exhibited by land-plants. The clefts in the rocks of quartziferous slate in the Central Alps are, in many places, overgrown by saxifrages (*Saxifraga Sturmiana* and *Saxifraga oppositifolia*) with leaves aggregated together in closely-crowded rosettes, which are conspicuous from afar, owing to their pale colouring. On closer inspection one finds that the apices and edges of these rosulate leaves are covered with little incrustations of carbonate of lime, a substance which will be frequently referred to in connection with its importance to plants. But one seeks in vain for any lime compound in the earth which fills the clefts, and the only traces of lime contained in the adjacent rock itself are those occurring in the little scales of mica scattered about, and these are not readily decomposable. Yet the lime incrusting the saxifrage leaves can only be derived from the underlying rock, just as in former instances the silicic acid in the cell-membranes of diatoms must be secreted from the spring described, the iodine in sea-weeds from the sea, and the common salt in water-lilies from the pond where they grow, although in each case the substance concerned is only to be found, if at all, in scarcely ponderable traces in the soil or liquid serving as medium. Facts of this kind have a special interest, because they prove that plants have the power of appropriating a substance, if it is important to them, even when it is only present in extremely minute quantities. Where a plant is surrounded by liquid, we can well imagine that fresh portions of the medium are constantly coming into contact with its surface; for, even in water apparently still, compensating currents are continually being caused by changes of temperature. Thus, in the course of a day, thousands of litres of sea-water may flow over a sea-weed with a surface of one square meter, and, even if only a small portion of the substance, traces of which we are supposing to exist in the water, is wrested from each litre, still, the absorbing plant might collect quite a profitable quantity in a number of days. The volume of water flowing over a plant situated in the source of a spring is still greater, and it is readily conceivable that even the most minute trace of silicic acid may become of account in course of time. There is more difficulty in understanding how plants with roots in the earth set about utilizing substances contained in the soil in scarcely appreciable quantities. These plants

must at all events come into contact with as great a mass of nutrient soil as possible, and this is effected by means of a widely-ramifying system of roots; and, in addition, they must assist in making available desirable matter in the soil by the elimination from themselves of certain substances.

In order to explain the remarkable power that plants possess of exercising a choice in the absorption of certain food-stuffs from amongst the whole number presented to them, we must in the first place assume a special structure to exist in the cells which are in immediate contact with the nutrient medium. To reach the interior of a cell, the salts must pass through the cell-membrane and the so-called ectoplasm. We may look upon these walls, that are to be penetrated, as filters, or, to abide by our previous simile, as sieves, which allow only certain kinds of molecules to pass and arrest others. Moreover, just as the structure of a sieve, especially the size and shape of its pores, has its effect in the separation of the particles of the matter sifted, so also may the structure of a cell-wall have a discriminating influence in the absorption of food-salts. It may be supposed that the cell-wall in one species of plant acts as a sieve capable of letting through molecules of potash but none of alumina, whilst the cell-wall in a second species allows molecules of alumina to pass as well, but is impervious to those of chloride of sodium. This hypothesis would also explain why the absorption of food-stuffs by plants generally takes place through cell-walls, and why absorption into the organs concerned by means of open tubes, which would be at all events a much simpler method, is not preferred. It is, however, necessary to investigate first the nature of the force which causes molecules of the various salts to move from the soil to the cell-membranes, which we suppose to be like sieves, and through them into the interior of a plant. A force acting in this sense from without is inconceivable, and we must therefore look for the motive stimulus in the plant itself.

As has been already stated in connection with the absorption of carbonic acid, it is believed that the cause of this movement is the disturbance of the molecular equilibrium in the growing vegetable organism. If at one spot in the protoplasm of a cell a particular substance is altered, and, let us say, converted into an insoluble compound, the previous grouping of molecules appears to be altered, or in other words, the molecular equilibrium is disturbed. To restore equilibrium, there must be a re-introduction of molecules of the material that has been removed; and the attraction of them from the quarter where they occur in a fluid, that is to say in a mobile condition, is the more energetic. Supposing, for instance, gypsum (*i.e.* sulphate of lime) is being decomposed within a cell, and the lime combines with the oxalic acid (set free in the same cell) to form insoluble oxalate of lime, whilst the sulphur combines with other elements to form insoluble albuminoids, this use of the gypsum occasions a violent attraction of that substance from the environment, or, to put it another way, it causes a movement of gypsum towards the place of consumption. If this latter place is a cell in immediate contact with the nutrient substratum, the absorption of the substance

attracted is direct; but if the cell in which the material is used up is separated from the substratum by intervening cells, the attraction must act through all those cells upon it. The substance consumed must be taken in the first place from the cell adjoining the consuming cell on the side towards the periphery; this cell again must take it from its neighbour, which is still nearer the periphery, and so on until the external cells themselves exercise their influence upon the nutrient substratum. Thus, one may regard the growing cells in which substances are used up, as centres of attraction with respect to those substances. This also explains why it is that the influx of food-salts takes place only so long as the plant is growing; and we see, too, that the direction of the current must vary according to the position of the growing cells, and according to the degree of their constructive activity.

But that one plant prefers one substance and another another—that one species attracts iodine, a second sodium, and a third iron—can only be interpreted as a result of the specific constitution of the protoplasm. The protoplasm of a growing cell which contains no iodine does not require that substance either, for the processes of transmutation and storage. A protoplast of this kind will not therefore be a centre of attraction for iodine, but will draw from the environment with great force substances which are its essential constituents. Having gained this conception of the absorption and selection of food-salts, we are able to imagine the possibility of a substance being sought after by one species whilst acting as poison on another. Iodine itself exercises a prejudicial effect on many plants, even when present in very small quantities. Cell-membranes in immediate contact with a medium containing iodine are modified as regards their structure by the iodine: their pores are enlarged, lose their value as orifices adapted to the admittance of certain food-salts in limited quantities, and they no longer prevent the influx of injurious substances. Ultimately they die, and by so doing the entire plant suffers. On the other hand, plants to which iodine is an indispensable constituent are not hurt in any way by the presence of small quantities of this substance in the nutrient medium: their cell-membranes are neither paralysed nor destroyed, and suction is able to take place through them in a perfectly normal manner. But we must in this case specially emphasize the condition of the amount being small, for a larger quantity of this substance is positively injurious even to plants which require iodine.

The general rule for a great number of plants is that they thrive best when the food-salts necessary to them are supplied in very dilute solutions. An increase in the quantity of the salts administered not only fails to promote development, but, on the contrary, arrests it. This is the result even if the salts are such as are absolutely necessary in small quantities to the plants in question. A very minute amount of an iron salt is indispensable to all green plants; but, if a certain measure is exceeded, iron salts have a destructive effect on the cell-membranes and protoplasm, and cause the plant to die. But at what point the boundary lies between salubrious effects and the reverse, where the beneficial action of particular

substances ceases and detrimental action begins, is not known more precisely than has been stated. We only know that different plants behave very differently in this respect. Suppose, for example, that we scatter wood-ash over a field which is overgrown by grasses, mosses, and various herbs and shrubs. The result is that the mosses die; in the case of the grasses growth is somewhat increased; whilst some of the herbs and shrubs, notably polygonaceous and cruciferous plants, exhibit a strikingly luxuriant growth. If we scatter gypsum instead, the development of clover is enhanced, and, on the other hand, there are certain ferns and grasses that die earlier when gypsum is supplied, or, at least, are considerably stunted in their growth.

The fact that certain plants predominate on calcareous and others on siliceous ground has been the subject of very thorough investigation; and these researches were regarded as justifying the assumption that particular species require a more or less considerable quantity of lime for food, whilst others require similarly silicic acid. Hereupon was founded a division of plants into those which required and were tolerant of lime, and into such as required and tolerated silica. The explanation given of these facts does not seem, however, to be satisfactory, at any rate in the case of siliceous plants. It is much more probable that the so-called silica-loving plants are produced on ground composed of quartz, granite, or slate, not by reason of the abundance of silicic acid, but because of the absence of lime in any large quantity, such as would be liable to injure plants of the kind; for only traces of lime are found, and its presence to this extent is absolutely necessary for every plant. This is not of course inconsistent with the fact that individual species require larger quantities of particular food-salts and only flourish luxuriantly when these nutritive salts are not meted out too sparingly. In the case of oraches, thrifts, wormwood species, and cruciferous plants, alkalies, in comparatively large quantities, are necessary for hardy development. The proper habitat for these plants, therefore, is on soils which contain an abundance of easily soluble alkaline compounds, in places where the ground is regularly saturated by saline solutions, and where crystals of salt effloresce on the drying surface. Such places are the sea-shore, the salt steppes, and the neighbourhood of salt-mines. The above plants not only flourish in these localities in great abundance and perfection, but they supplant all other species on which the excessive provision of soluble alkaline salts is not beneficial. If the seeds of such plants happen to fall upon the salt ground they germinate, but only drag out a miserable existence for a short time, and in the end are crowded out by the luxuriant oraches and crucifers. Plants which only flourish abundantly on soils rich in alkaline salts are called halophytes. The same name has also been applied to plants which only thrive in sea-water. Most of the species used by us as edible vegetables, as, for instance, cabbages, turnips, cress, &c., are really descended from halophytes, and accordingly require a soil that contains a comparatively rich supply of alkalies. An opportunity will occur, later on, of returning to the question as to how far agriculture has gained by all these discoveries, and of considering what processes, based upon

the results of scientific research, have been introduced into practice. Amongst these processes may be mentioned the rotation of crops, the artificial application of manure to exhausted land, and the restitution of the mineral food-salts which the particular plants last cultivated have withdrawn from the land under tillage.

## ABSORPTION OF FOOD-SALTS BY WATER-PLANTS.

It is usual to designate all plants that grow in water as hydrophytes or water-plants. But in their narrower sense these names are only applicable to those plants which, during their entire lives, vegetate under water and derive their nutriment, especially carbonic acid, direct from the water. A number of plants have widely ramifying roots fixed in the earth at the bottom of water, and the lower parts of their stems, either temporarily or throughout life, immersed in water, whilst the upper parts of their stems and their upper leaves are exposed to the air and take carbonic acid direct from the atmosphere, and these should be regarded as marsh-plants and classed with land-plants so far as regards food-absorption. Reeds and rushes, water-fennel and water-plantain, the yellow water-lily, even the amphibious *Polygonum* and the white water-lily, are marsh-plants and not true hydrophytes. It is characteristic of all these marsh-plants, that if they are entirely submerged for any length of time they die, whereas they are not injured if the water's level at the place where they grow sinks so as to expose the lower portions of the stem. In places formerly submerged, but from which, in course of time, the water has retreated, so that they have been turned into meadows, one may come across not only clumps of reeds and rushes but even yellow and white water-lilies, flourishing perfectly on the moist earth.

Water-plants, or hydrophytes in the proper acceptation of the term, perish if they are kept for a length of time out of their proper medium and exposed to the air. In most of them death ensues quickly, for their delicate cell-membranes are not able to prevent the exhalation of water from the interior of their cells; and, there being no provision for a replacement of the evaporated fluid, the whole plant dries up. If one supplies aquatic plants, thus desiccated, with water, though it is indeed absorbed it no longer has the power of reviving them. Those hydrophytes which occur in the sea, near the shore, are able to stand exposure to the air for a comparatively long time, and they are regularly subject to it during ebb-tide. Sea-wracks which at high-tide were floating in the water are then seen lying on the dry rocks or sand of the shore. But the membranes of the cells forming the outermost layer in all these sea-wracks is very thick. They retain water staunchly and prevent the plants from drying up, at least until high-tide occurs again, when they are once more submerged.

Amphibious plants in which the lower leaves are like those of aquatics and the upper like those of land-plants so far as desiccation is concerned (e.g. several kinds of pond-weed—*Potamogeton heterophyllum* and *P. natans*—and a few white-flowered Ranunculi—*Ranunculus aquatilis* and *R. hololeucus*), exhibit a transition stage from

aquatic plants to land-plants. When the water sinks and they are finally left lying exposed on the mud or wet sand, to which they appear to be firmly attached by their abundant roots, it is only the previously submerged leaves that dry up. That part of the foliage which floated on the surface and was consequently always in contact with the air continues to thrive, and any fresh leaves that may be developed adapt themselves completely to the new environment. Similar behaviour is observed in many of the plants which float freely on the surface of water. Such, for instance, is the case with some species of duckweed (*Lemna minor* and *L. polyrrhiza*), with *Azolla*, *Pontederia* and *Pistia*; they do not die when the water sinks, leaving them stranded, but absorb food-stuffs from the wet earth through their roots, and in this condition are not to be distinguished from land-plants.

Hydrophytes in the narrow sense, i.e. plants which are entirely submerged and die if they are surrounded by air instead of water for any length of time, are for the most part fixed to some support beneath the water. In many cases the characteristic method of reproduction consists in the separation of special cells, which then swim about for a time in the water. Sooner or later, however, they re-attach themselves to some seemingly suitable spot, and the further phases of their development are again stationary. Comparatively few permanently submerged species are freely suspended in the liquid medium in every stage of development. Such free plants are liable to be shifted by currents in the water, but the extent of their displacement is never very great, owing to the fact that submerged species of this kind occur almost exclusively in still water. As instances may be mentioned the ivy-leaved duckweed (*Lemna trisulca*), the water-violet (*Hottonia palustris*), the various species of hornwort (*Ceratophyllum*), in all of which roots are absent; and in addition amongst the lower or cryptogamic plants *Riccia fluitans*, and many of the Desmidiaceæ, Spirogyras and Nostocineæ.

Some of these aquatic plants periodically rest on the bottom of the pond or lake in which they live. An example is afforded by the remarkable plant known as the water-soldier (*Stratiotes aloides*), which, as is indicated by its Latin name, is not unlike an aloe in appearance. During the winter, this plant rests at the bottom of the pond it inhabits. As April draws near, the individual plants rise almost to the surface and remain floating there, producing fresh sword-shaped leaves and bunches of roots which arise from the abbreviated axis, and finally flowers which, when the summer is at its height, float upon the surface. When the time of flowering is over, the plant sinks again to mature its fruit and seeds, and develop buds for the production of young daughter-plants. Towards the end of August, it rises for the second time in one year. The young plants that have meantime grown up resemble their parent completely, except that their size is smaller. They grow at the end of long stalks springing from amongst the whorled leaves, and the stately mother-plant is now surrounded by them like a hen by her chickens. During the autumn, the shoots connecting the daughter-plants with their parent rot away, and, thus isolated, each little rosette, as well as the mother-plant, sinks once more to the bottom of the pond and there hibernates.

Altogether the number of submerged plants which live suspended in water is very small. As has been said before, by far the greater number are attached somewhere. Seed-bearing plants or Phanerogamia, such as *Vallisneria*, *Ouviranda*, *Myriophyllum*, *Najas*, *Zannichellia*, *Ruppia*, *Zostera*, *Elodea*, *Hydrilla*, and several species of *Potamogeton* (*P. pectinatus*, *P. pusillus*, *P. lucens*, *P. densus*, *P. crispus*); as also Cryptogamia, such as the various species of *Isoetes* and *Pilularia* and submerged mosses, are fastened in the mud under water by means of attachment-roots or of rhizoids, whilst the almost illimitable host of brown and red sea-weeds are fixed by special cells or groups of cells, which are often root-like in appearance. The sea-weeds choose rocks and stones, by preference, for their support, but they also make use of animals and plants. The shells of mussels and snails are often completely overgrown by brown and red sea-weeds. Larger kinds of Fucaceæ, especially the species of *Sargassum* and *Cystosira*, which form regular submarine forests, bear upon their branches numerous other small epiphytes, chiefly Florideæ, and these again are themselves covered by minute Diatomaceæ. Many of the huge and lofty brown sea-weeds which raise themselves from the bottom of the sea, remind one forcibly of tropical trees covered with Orchidææ and Bromeliaceæ, whilst the latter are themselves overgrown by Mosses and Lichens. These epiphytes are for the most part, however, neither parasitic nor saprophytic. In general hydrophytes attached by means of single cells or groups of cells derive no nutriment, i.e. no food-salts, from the support they rest upon. When loosened from the substratum they continue to live in the water for a long time; they increase in size, and if they come into contact with a solid body are apt to attach themselves to it. In this connection it is well worthy of remark that certain Crustacea have their carapaces entirely covered by hydrophytes of this kind, and that it takes a very short time for the plants to establish themselves upon them. For instance, some species of crabs, such as *Maja verrucosa*, *Pisa tetraodon* and *P. armata*, *Inachus scorpioides* and *Stenorhynchus longirostris*, cut off bits of Wracks, Florideæ, Ulvæ, &c., with their claws, and place them on the top of their carapaces, securing them on peculiar spiky or hooked hairs. The fragments grow firmly to the crabs' chitinous coats, and far from being harmful to the animals are, on the contrary, an important means of protection. The crabs in question escape pursuit in consequence of this disguise, and it is to be observed that each species chooses the very material which makes it most unrecognizable to plant upon the exterior of its body: those species which live chiefly in regions where Cystosiras are indigenous deck themselves in Cystosiras, whilst those which inhabit the same places as Ulvæ, carry Ulvæ on their backs. This phenomenon has for us a special interest in that it shows that the water-plants we are discussing draw no food-salts from their place of attachment, and that accordingly the chemical composition of the support is a matter of utter indifference to all these Fucaceæ, Florideæ, Ulvæ, &c.

There is no doubt that food-salts are absorbed by these hydrophytes from the surrounding water through their whole surface. Accordingly the structure of their peripheral cells is much simpler than is the case in land-plants. In the latter very

complicated adaptations are necessary for the extraction of food-salts from the earth. In particular, the portions which are exposed to the air above ground exhibit a number of special structures connected with this extraction. These structures (cuticle, stomata, &c.) are superfluous in the case of aquatic plants, for there is with them no necessity for raising and conducting food-salts into the parts where they can be used up. Moreover the absorption of nutritious matter is much simpler, inasmuch as it is not necessary for the absorbent parts to search for a perpetual source of the requisite substances. The roots of land-plants have often to range over a wide area in order to find sufficient nourishment in the earth, and frequently they have then to liberate it, *i.e.* bring it into a state of solution. This is not the case with water-plants. They are completely surrounded by a medium which is itself to a large extent a solution of food-salts, and no sooner are substances withdrawn by the absorbent cells from the layers of water immediately bounding them than those substances are again supplied from the more remote environment. Constant compensating currents occur in water, and there is, therefore, scarcely an aquatic plant towards which there is not a perpetual flow of the food-salts it requires in a form suitable for absorption. In connection with this kind of food-absorption there is also the fact that the parts by which hydrophytes attach themselves to a support are relatively small in area. Fucoids, as large as hazel trees in height and girth, are fixed to submerged rocks by groups of cells perhaps only 1 cm. in diameter.

The quantity of food-salts absorbed by hydrophytes is very considerable compared with the amounts absorbed by other plants. As has been mentioned before, soda and iodine play a very important part in the thousands of different varieties which live in the sea. If Florideæ are transferred from the sea into pure distilled water, common salt and other saline compounds diffuse out of the interior of the cells through the cell-membranes into the fresh water around. The red colouring matter of these Florideæ also passes through the cell-walls into the water, proving that the molecular structure of the membrane is adapted to the agency of salt water in the osmotic processes of food-absorption.

Plants living in fresh, or in brackish water, likewise absorb relatively large quantities of food-salts; and this accounts for the fact that water which is very poorly provided with nutriment of the kind contains only very few vegetable species.

One would expect that exceedingly abundant vegetation would be evolved in running water, provided the latter contained food-salts in solution, however small they might be in quantity. For, in such a situation, it is not necessary to wait for the salts withdrawn by the plants from their immediate environment to be restored by the slow processes of mixture and equilibration; the water which has been drained of nutriment is replaced the next moment by other water bearing fresh food-salts. Experience shows, however, that flowing water is not so favourable to the development of hydrophytes as is the still water of pools, ponds, and lakes. This may partly depend on the fact that running water is always poorer in food-salts, and

partly also on the circumstance that mechanical difficulties are opposed to the taking up of saline molecules from water in rapid motion. There are only a few plants that are able to absorb under these conditions, and these choose, by preference, the very spots where they are most exposed to the dash of the water. Thus, certain *Nostocineæ* (*Zonotrichia*, *Scytonema*) are to be found constantly in waterfalls at the parts where the most violent fall occurs. *Lemania*, *Hydrurus*, and many mosses and liverworts, grow by preference in the foaming cascades of rapid torrents. Amongst flowering plants we only know of the *Podostemaceæ* as choosing a habitat of this kind. *Podostemaceæ* are exceedingly curious little plants, which at first glance one would take for mosses or liverworts without roots. Some of them, e.g. the Brazilian species of the genus *Lophogyne* and the various species of *Terniola* growing in Ceylon, exhibit no differentiation into stem and leaves, but are only represented by green fissured and indented lobes attached to stones. They belong without exception to the tropical zone, and occur there in the beds of streams, attached to rocks, over which the foaming water rushes.

## ABSORPTION OF FOOD-SALTS BY LITHOPHYTES.

Nothing would seem more natural, as to the absorption of mineral salts by lithophytes, than that the stone which constitutes their support should yield the salts, and that the attached plants should suck them up; but, generally speaking, the case is not so simple. There are mosses and lichens which cling to the surfaces of rocks on mountain tops. These rocks are sometimes composed of perfectly pure quartz, and yet the plants in question contain very little silica; they contain, on the other hand, a number of substances entirely wanting in the composition of the underlying rock, and which could not, therefore, have been derived from that source. For many of these lithophytes the rock is, in the main, only a substratum for attachment, and in no way a nutrient soil; just as, in the case of many aquatic plants, the stones to which they cling by their discs of attachment are anything but sources of nourishment.

From what source, then, do stone-plants of this kind derive the food-salts which are wanting in their substratum? It may sound paradoxical, but it is nevertheless the fact, that they obtain those salts from the air through the medium of atmospheric precipitation. Rain and snow not only absorb carbon dioxide, sulphuric acid, and ammonia—which occur in air universally, although in extremely minute quantities—but they also collect, as they fall, floating particles of dust. The opinion is widely entertained that although the atmosphere is full of dust in the neighbourhood of cities and human settlements generally, where the soil is laid bare and ploughed up, and roads and paths have been made for purposes of traffic, and perhaps also over steppes and deserts where large areas of ground are destitute of vegetation, yet that there is no dust in the air over land remote from places of that kind or in the air of marshes, lakes, or seas. This notion has certainly some warrant if we regard as dust only the coarser particles which are raised from loose earth and

whirled into the air by the wind. Moreover, the quality of the dust will no doubt be characteristically affected by the vicinity of areas of industry. One has only to look at the sooty leaves and branches of trees in parks near manufactories to convince oneself of the reality of this influence. But it would be quite erroneous to suppose that the air in regions far from land that has been cultivated or otherwise opened up is free from dust. It contains dust everywhere. There is dust in the air of the extensive ice-fields of arctic regions and of high mountain glaciers, and there is dust in the air of great forests and over the boundless sea.

If the rays of the setting sun fall obliquely through a gap between two peaks in a wood-clad mountain valley, sun-motes may be seen floating up and down and in circles, just as they do in a room when the last rays before sunset fall through the window. These motes are of course not usually visible, and they are moreover much smaller than the particles of dust which are raised by the wind from roads and then again deposited. Now, when rain falls, it takes the sun-motes from the air and brings them down to earth, and the air is thus washed to a certain degree of purity. This happens still more completely in the event of snow. The latter acts not unlike a mass of gelatine used to purify cloudy liquids, its effect being to drag down with it all the particles to which the turbidity is due, leaving the upper part of the liquid quite clear. Similarly, falling snow-flakes filter the air; and, mixed with fallen snow, there are accordingly innumerable particles of dust. If afterwards the snow gradually melts, it dissolves some of the dust, which then drains away into chinks and depressions; but a portion remains behind undissolved. This portion is gradually consolidated, and then appears lying on the parts of the snow that are still unmelted in the form of dark patches, streaks, and bands; often also it forms a smeary graphitic covering so widely spreading over the last remnants of melting snow that the latter resemble lumps of mud rather than snow. Accordingly we find it everywhere—in regions cultivated and uncultivated, in tilled lowlands and on high grassy plains above forest limits, where no tilled land is to be seen in any direction, and lastly in arctic regions in the middle of glaciers several miles across.

All this snow dust is not invariably deposited as a result of the filtering of the air by falling snow-flakes; an additional supply is brought by the winds which blow across the snow-fields. It is not of rare occurrence in the Alps for snow-fields to exhibit suddenly, after violent storms, an orange-red coloration. On closer inspection one finds that the surface of the snow is strewn with a layer of powder, infinitesimally fine and for the most part brick-red, which has been brought by the gales. Investigation of this "meteoric dust" shows that it is composed chiefly of minute fragments of ferruginous quartz, felspar, and various other minerals. Mixed with these there are, however, sometimes remnants of organic bodies, such as bits of dead insects, siliceous skeletons of diatoms, spores, pollen-grains, tiny fragments of stems, leaves, and fruits, and the like. Once, after a south wind had prevailed for several days, the snow-fields of the Solstein range near Innsbruck were covered, at a height of from two to three thousand meters above the sea-level,

with millions of a species of *Micrococcus*, which lent a rosy hue to vast expanses of snow.

Most of the dust in the atmosphere originates, doubtless, from our earth. The air that blows in waves over the earth can carry along with it not only dead and detached portions of plants, but also loose particles of rock, sand, earth, and dried mud. If one draws one's palm across the weather side of a dry rock composed of dolomitic limestone, gneiss, trachyte, or mica-schist, the surface of the stone always feels dusty, and the slightest movement of the hand is sufficient to detach a number of particles which were already separate from the rock and only held in loose connection with it. This dust is liable to be detached and carried away by any strong gust of wind. Larger and heavier particles are not, it is true, lifted much above the ground; they are rolled and pounded along and thereby reduced to a still finer powder. This finer dust may then be scattered afar by gales blowing horizontally, or even ascend into higher atmospheric strata. The finest dust in particular, however, is carried up into the higher layers of the air by the currents which ascend from the earth in calm weather; and this applies not only to the tropics but to the temperate zones as well, and even to the frigid regions of the arctic zone. When, therefore, this dust is brought back by rain or snow from the upper aerial strata to the earth, it but completes a circuit. Indeed it is highly probable that the particles of dust restored to earth by means of atmospheric deposits recommence their aerial travels as soon as they are thoroughly dry again, and that there is thus a circulation of dust analogous to that of water.

There is of course no inconsistency in the fact that meteoric dust, which is often drifted along in surprisingly large quantities, may originate quite suddenly during volcanic eruptions; nay, it is even possible that cosmic dust reaches our atmosphere and thence falls to the earth. Chemical investigation of aerial dust has, no doubt, yielded in most cases only sulphuric and phosphoric acids, lime, magnesia, oxide of iron, alumina, silica, and traces of potash and soda, that is to say, the most widely distributed constituents of the solid crust of our earth; but cobalt and copper have also been found in it, over and over again, and it has hence been inferred that the dust in these cases was of cosmic origin.

In relation to the question which we have here to answer the above is, after all, almost a matter of indifference. The only important facts are that dust in a state of extremely fine division is blown about in the air, that this dust contains the salts required by plants for their food, that it is carried for the most part mechanically by drops of water and flakes of snow, condensed in the atmosphere, and is partially dissolved, that the atmospheric deposits supply lithophytic plants with a sufficient quantity of nutrient salts, and that the aqueous solution so supplied is rapidly absorbed by the whole surface of the plants in question. We must not omit to mention here that the demand of lithophytes for mineral food-salts is not very great. In particular the protonemæ and even the leafy shoots of *Grimmiæ*, *Rhacomitriæ*, *Andreæaceæ* and other rock mosses, and the *Collemaceæ* and most crustaceous lichens only contain very minute quantities of these substances. Water containing

the usual mineral salts in about such proportion as is necessary for the cultivation of cereals in fields has actually an injurious effect on these lithophytes and soon kills them.

At the end of this section we shall consider what happens to dust which is brought to earth from the air by rain and snow but is not dissolved, and the important part it plays in clothing the naked ground and in changes of vegetation. Here, however, it must be noted that most lithophytes are true dust-catchers, that is to say, they are able to retain, mechanically, dust conveyed to them by wind, rain, and snow, and to use it in later stages of development by extracting nutriment from it. Many mosses are completely lithophytic in early stages of development whilst later they figure as land-plants.

#### ABSORPTION OF FOOD-SALTS BY LAND-PLANTS.

In no class of plants is the absorption of mineral food-salts accomplished in so complicated a manner as in land-plants. Moreover, this absorption is by no means uniform in different forms of plants, and we must beware of generalizing with regard to processes which have only been traced and studied in isolated groups—perhaps only in the commonly distributed cultivated plants. On the other hand, with a view to synoptical representation, it is not desirable to enter into too great detail or to attempt to describe all the various differences minutely.

At the outset, it is difficult to give an accurate account of the soil which constitutes the source of nutriment in the case of land-plants. From the dark graphitic mass composed of sun-motes, which is deposited in the place of a melted layer of snow, to coarse gravel, there is an unbroken chain of transition stages; loam, sand and gravel are only specially-marked members of this chain. Again, just as earth varies in respect of the size of its component parts, so also it varies in the mineral salts it contains, in the amount of admixture of decaying vegetable and animal remains, in the nature of the union of its constituents, and in its capacity to absorb, to retain, or to yield up water. Compare the sand composed of quartz on the bank of a mountain stream with that of calcareous origin which is found impregnated with salt on the sea-shore, or with the sand at the foot of mountains of trachyte, which has an efflorescence of soda-salts. Or compare the granite bed of a desert, bare of soil, with the loam on the granitic plateaus of northern regions where there is an intermixture of the remains of a vegetation for centuries active. How great is the difference in each case! But whatever the kind of earth, it is only of value as a source of nutriment for a plant when the interstices of its various particles are filled with watery fluid for the time during which the plant is engaged in the construction of organic substances.

But how is the earth supplied with water?

“Das hat nicht Rast bei Tag und Nacht,  
Ist stets auf Wanderschaft bedacht.”

Streams fall into lakes, rivers into the sea, and hence the water ascends into the atmosphere in the form of vapour, and returns once more to earth as snow, rain, and dew. Through porous earth it percolates until it has filled all the interspaces. If its further descent be impeded by impervious strata, it spreads literally as subterranean water, or else comes up at some special spot as a spring. Earth which is richly endowed with decaying vegetable remains is able to absorb vapour in addition from the atmosphere. When this occurs, carbonic and nitric acids are always absorbed along with the aqueous vapour. These are contained, as has been mentioned before, in atmospheric deposits, and another source of these acids is afforded by the decay of dead parts of plants. Water precipitated from the atmosphere, and containing carbonic and nitric acids, is able by their means to decompose the compounds in all the rocks which come in its way as it percolates through the ground, especially when its action is long continued. The siliceous compounds or so-called silicates—feldspars, mica, hornblende, and augite in particular—and quartz, the anhydride of silicic acid, which form the preponderant mass of the rocks of the solid crust of our earth, either contain a great quantity of silica, alumina, and alkalies, or if they are relatively poor in silica they may be rich in iron. The former are found chiefly in granite, gneiss, mica-schist, and argillaceous slate; the latter preponderate in serpentine, syenite, melaphyr, dolerite, trachyte and basalt. First the feldspars are decomposed by the acid water. Their alkalies combine with the carbonic and nitric acids forming soluble salts, and the alumina and silica remain behind as clay. Iron is also converted into soluble salts. The most difficult substances to decompose are the mica and quartz, and it is on that account that they so often appear in the form of glittering scales and angular nodules mixed with the clay produced from the decomposition of feldspar. But, ultimately, even they are unable to withstand the continuous action of the acidulated water. The result of these chemical changes is an earth, which, according to the nature of the parent rock, contains a preponderating amount of clay, of quartzose sand or of mica, which is coloured in various ways by iron compounds. Of substances useful to plants these earths yield generally on analysis the following: potash, soda, lime, magnesia, alumina, ferrous and ferric oxides, manganese, chlorine, sulphuric acid, phosphoric acid, silica, and carbonic acid, sometimes one sometimes another in greater proportion relatively, and traces of many substances often so slight as hardly to be detected.

It is true that limestone and dolomite, which, next to the above-mentioned rocks, enter most largely into the composition of the solid crust of the earth, consist chiefly of carbonate of lime and magnesium carbonate respectively; but wherever they occur in extensive strata and piles, they always contain in addition an admixture of alumina, silicic acid, ferrous oxide, manganese, traces of alkalies in combination with phosphoric and sulphuric acids, &c. Of the carbonates of lime and magnesia a great part is gradually dissolved and carried away upon the invasion of water containing carbonic and nitric acids, and a proportion also of the substances mixed with them, as above mentioned, is lixiviated. What remains

behind then consists of an argillaceous, loamy mass, variously coloured by iron and very similar in appearance to the clay formed from the decomposition of felspar. According to the quantity of the substances mixed with the carbonate of lime in the rock, the loamy earth formed from limestone is either abundant or only in restricted layers, bands and pockets lying on, or intercalated within, the undecomposed débris of the stone. Chemical analysis has resulted in the discovery that there are, as a rule, in loamy earth of this kind the same ingredients available for plants as have been identified in earth produced from silicates; and we are led to believe that earths, collected in widely different places and covering rocks of most various kinds, are much more uniform qualitatively than has been supposed. Only, the relative proportions of the substances forming the mixture are usually different. Silica and the alkalies are less conspicuous in earth derived from limestone, and carbonate of lime in that which is formed from silicates. This difference is particularly striking in instances where the rock consisted almost entirely either of quartz and mica or of nearly pure carbonates of lime and magnesium. In these cases the earth formed is not argillaceous, but of loose consistence, very abundant, and composed, according to the kind of rock, of quartzose sand and mica scales or calcareous and dolomitic sand.

The conversion of rocks into earths by the action of water from the atmosphere containing carbonic and nitric acids is, besides, materially modified by the disruptions which ensue from changes of temperature, more particularly by the freezing of water within the pores of rocks. It is also affected, though more remotely, by the mechanical action of water and air in motion, and, lastly, by the plants themselves, which penetrate with their roots into the narrowest crevices and mingle their dead remains with the portions of the rock that are decomposed, broken up, or abraded by chemical and mechanical agencies. The substance produced from a rock in the manner explained is called earth-mould, or simply earth. The matter resulting from the decomposition of plants and animals is designated by the term "humus." Earth which includes an abundance of decomposed fragments of plants, *i.e.* has a large admixture of humus, is called vegetable mould.

Every kind of earth, but especially earth rich in humus and clay, has the power of retaining gases, and especially water and salts. When water containing salts in solution is poured over a layer of dry vegetable mould, it percolates into the spaces between the particles of earth, and speedily drives out of them the air which has but slight adhesion, and which then ascends in bubbles. It is not till all the inter-spaces are full of water, whilst a fresh supply is constantly maintained from above, that any of the liquid oozes out from beneath the stratum of earth. The water remaining in the interstices is held there by adhesion to the particles of earth, and we must conceive each of these particles as surrounded by an adherent film of water. The inorganic salts, infiltrating with the water, are held with still greater energy. The water which trickles from the bottom of the earth always contains a much smaller proportion of salts in solution than that which was poured on above, whence we conclude that the latter are in part absorbed by the earth.

The salts are to be regarded as forming an extremely delicate coating round minute particles of earth where they are forcibly retained. If a plant rooted in the earth is to take in these salts it has to overcome the force by which their molecules are detained. This is effected, however, by means of a very powerful attraction exerted by the protoplasts of the plant as they grow, carry on the work of construction, and use up material. What actually happens is an energetic suction by the cells that are in close contact with particles of earth. This suction depends, however, upon the chemical affinity between the substances in the interior of the cells and the salts adhering to the earth-particles, as well as upon the consumption of food-salts for the manufacture of organic compounds within the green cells. It is supposed that whenever salts are abstracted from soil-particles by suction, a restitution of like salts immediately takes place, particles still unresolved in the immediate neighbourhood being dissolved, and a fresh influx taking place from the environment. Consequently the concentration of the solution retained by the earth is always approximately the same, or, at any rate, equilibrium is very quickly restored. One advantage of this is that the cells in immediate contact with particles of earth, and their adherent liquid, can only meet with a saline solution of constant weak concentration, and are therefore secure from injury such as would result in the case of most plants, from contact with a very concentrated solution. In other words, the absorptive power of earth acts as a regulator of the process of absorption of food-salts by plants, and is the means of keeping the saline solution in the earth always at the degree of strength best suited to the plants concerned.

Naturally, the passage of salts from the earth to the interior of a plant is dependent on the aid of water containing both the substances composing cell-contents and the food-salts in solution. The cell-membranes, through which absorption takes place, are saturated with this solution. The aqueous films adhering to the particles of earth, the water saturating the cell-membrane, and the liquid inside the cells are really in unbroken connection, and along this continuous water-way the passage of salt molecules in and out can take place easily.

The absorption of food-salts directly from the earth by green cells occurs very rarely. The protonema of *Polytrichum*, which spreads its threads over loamy earth and wraps it in a delicate green felt, and that of the famous Cavern Moss (*Schistostega*), whose long tubular lower cells penetrate the earth in the recesses of caves, do undoubtedly suck up their necessary food-salts by means of cells containing chlorophyll. A drawing of the latter is given in Plate I., fig. p.

The majority of land-plants have, however, special absorptive cells for the taking-up of salts in solution. These cells are imbedded amongst or lodged upon the earth-particles, and are usually in intimate connection with portions of them. Any part of a plant that penetrates into the earth or lies upon it, may, if it performs the function of absorption, be equipped with cells of the kind. *Plagiothecium nekeroideum*, a delicate moss belonging to the flora of Germany, and growing on earth under overhanging rocks, where it is not exposed to rain, and therefore cannot receive any food-salts through that agency, develops absorption-cells on the apices

of its green leaflets. So also does *Leucobryum javense*, a species native to Java. Several delicate ferns of the family of the *Hymenophyllaceæ* exhibit them on their subterranean stems. Many liverworts and the prothalli of ferns bear them on the under surfaces of their flat thalli which lie outspread on damp earth. But most commonly of all are they to be found close behind the growing tips of roots. Their form does not vary very much. On the roots of plants fringing the sources of cold mountain-springs, as on those of many marsh-plants in low-lying land, they are in the form of comparatively large, oblong, flattened, closely united cells, with thin walls and colourless contents. In some conifers, whilst having in the main the shape just described, they differ in that they are arched outwards so as to form papillæ; but in most other phanerogams the external cell-wall projects outwards, and the whole absorptive cell develops into a slender tube, set perpendicularly to the longitudinal axis of the root (fig. 12<sup>4</sup>).

Seen with the naked eye, or but slightly magnified, these delicate tubes look like fine hairs, and have received the name of "root-hairs." The end of a root often appears to be covered with velvety pile, and the absorptive cells are then very closely packed; more than four hundred per square millimeter have been occasionally counted. In other cases, however, there are hardly more than ten on a square millimeter. When in such small numbers they are usually elongated and clearly visible to the naked eye. Their length, for the most part, varies from the fraction of a millimeter to three millimeters, and their thickness between 0·008 m.m. and 0·14 m.m. It is only exceptionally that one meets with plants, rooted in mud, possessing root-hairs 5 m.m. or more in length. The absorptive cells of phanerogams are almost always simple epidermal cells of the particular part of the plant that bears them, and are not partitioned by any transverse walls. In mosses and fern prothalli, on the other hand, the absorption-cells are generally segmented by transverse septa and are usually greatly elongated. In those liverworts which belong to the genus *Marchantia* they form a thick felt on the under side of the leaf-like plant, or rather, on such part of it as is turned away from the light, and some of these tangled rhizoids attain a length of nearly 2 c.m. The stems of many mosses also are wrapped in a regular felt. This property is rendered very striking in the species of *Barbula*, *Dicranum*, and *Mnium*, and especially in such forms as have bright green leaves, by the reddish-brown colour of the cells in question. Sometimes the long capillary cells of which the felt is composed are twisted together spirally like the strands of a rope. A good instance of this is *Polytrichum*. These fine, hair-like, segmented and branched structures, found on mosses, variously matted and intertwined, are called rhizoids. But only those cells which come into contact with the earth-particles are truly absorbent. The rest do not serve to imbibe from the ground, but to conduct the aqueous solution of food-salts, after it has been taken up by the absorptive cells, to the stem and to the leaves.

The tubular cells resulting from the development of a root's epidermis are placed, as before observed, at right angles to its longitudinal axis. They only grow, however, in earth that is very damp, and even then their course is not always a straight

line, for as a rule they describe a spiral as they elongate. Their movement seems as though it were for discovering the most favourable parts of the earth for absorption and attachment. In this manner they penetrate into the interspaces in the earth which are filled with air and water. They also have the power of thrusting aside minute particles of earth, especially if the latter consists of loose sand or mud. If they strike perpendicularly a solid immovable bit of earth, they bend aside and grow round it with their surfaces closely adpressed to that of the obstacle until they reach the opposite point on the other side, when they once more resume their original direction (fig. 12<sup>3</sup>). When they encounter large grains of earth they

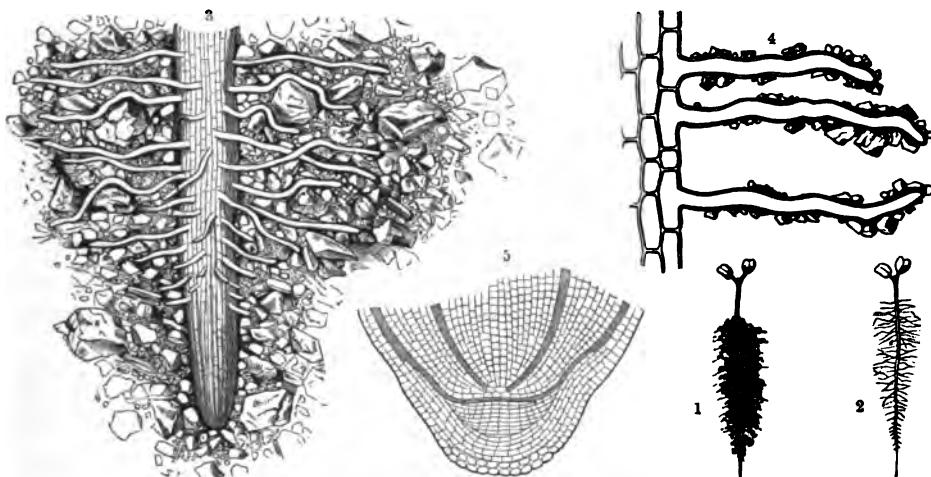


Fig. 12.—Absorptive Cells on Root of *Penstemon*.

<sup>1</sup> Seedling with the long absorptive cells of its root ("root-hairs") with sand attached. <sup>2</sup> The same seedling; the sand removed by washing. <sup>3</sup> Root-tip with absorptive cells;  $\times 10$ . <sup>4</sup> Absorptive cells with adherent particles of earth. <sup>5</sup> Section through the root-tip;  $\times 60$ .

sometimes stop and swell up to the shape of a club. The club divides into two or more arms, which grasp and cling to the granule like the fingers of a hand. Many fragments of earth remain thus in the grasp of finger-like processes, whilst others are held fast in the knots and spirals of corkscrew-shaped root-hairs which are often found tangled together. But the retention of most of the earth-particles which adhere to a plant, including fragments of lime, quartz, mica, felspar, &c., as well as plant-residues, is due to the fact that the outermost layer of the absorptive cells is sticky, it being altered into a swollen gelatinous mass which envelopes the particles. When this sticky layer becomes dry it contracts and stiffens, and the granules partially imbedded in it are thereby cemented so tightly to the absorptive cells that even violent shaking will not dislodge them.

In the case of most seedlings, and in that of grasses, the absorptive cells which proceed from the roots and which are especially numerous in the latter, are generally thickly covered with particles of earth (see fig. 12<sup>4</sup>). If such a root is pulled out of sandy soil it appears to be completely encased in a regular cylinder of sand (fig. 12<sup>1</sup>). A root of *Clusia alba*, taken from coarse gravel, had its root-hairs so tightly

adherent to bits of gravel that several little stones, weighing 1·8 grms., were found clinging to it when it was lifted. The gelatinous mass, resulting from the swelling-up of the external coat of the cell, does not in any way hinder absorption or the passage of food-salts in solution. Nor does the inner coat, the thickness of which varies between 0·0006 m.m. and 0·01 m.m., constitute any impediment to imbibition.

In addition to the absorption of nutritive salts by root-hairs, there is also, in many cases, an interchange of materials; that is to say, not only do substances infiltrate from the earth into the absorption-cells, and so onward into the tissues of a plant, but others pass out of the plant through the absorptive cells into the earth. Amongst these eliminated substances, carbonic acid, in particular, plays an important part. A portion of the earth-particles adhering to root-hairs are decomposed by it, and food-salts in immediate proximity to those cells are hereby rendered available and pass into the plant by the shortest way.

Having now seen that land-plants take in food-salts by means of special absorptive cells, it is natural to find that each of these plants develops its absorption-cells, projects them, and sets them to work at a place where there is a source of nutritive matter. The parts that bear absorptive cells will accordingly grow where there are food-salts and water, which is so necessary for their absorption. The *Merchantias* and fern prothalli spread themselves flat upon the ground, moulding themselves to its contour. From their under-surfaces they send down rhizoids with absorptive cells into the interstices of the soil. Roots provided with root-hairs behave similarly. If a foliage-leaf of the Pepper-plant or of a *Begonia* be cut up, and the pieces laid flat on damp earth, roots are formed from them in a very short time. The roots on each piece of leaf proceed from veins near the edge, which is turned away from the incident light, and grow vertically downwards into the ground.

It is matter of common knowledge that roots which arise upon subterranean parts of stems, like those formed on parts above-ground, grow downward with a force not to be accounted for by their weight alone. This phenomenon, which is called positive geotropism, is looked upon as an effect of gravitation. The idea is that an impetus to growth is given by gravity to the root-tip, and that a transmission of this stimulus ensues to the zone behind the tip where the growth of the root takes place. It is noteworthy that if bits of willow twigs are inserted upside down in the earth, or in damp moss, the roots formed from them, chiefly on the shady side, after bursting through the bark, grow downwards in the moist ground, pushing aside with considerable force the grains of earth which they encounter. The appearance of a willow branch thus reversed in the ground is all the more curious inasmuch as the shoots, which are developed simultaneously with roots from the leaf-buds, do not grow in the general direction of the buds and branches, but turn away immediately and bend upwards. Thus the direction of growth of roots and shoots produced on willow-cuttings remains always the same, whether the base or the top of the twig used as a cutting is inserted in the earth. A similar phenomenon is observed if the leafy rootless shoot of a succulent herb (*e.g. Sedum reflexum*) is cut

off and suspended in the air by a string. Whether it hangs with the apex uppermost, *i.e.* in the position in which it grew naturally, or with the apex towards the ground, it always, in a short space of time, produces roots which spring from the axis between the fleshy foliage-leaves and bending sharply grow to the earth. Thus in the former case their direction is contrary to the apex of the shoot; in the latter, curiously enough, it is in the same direction. If the height at which the shoot is suspended is only 2 c.m. above the earth, the roots growing towards the ground develop their root-hairs 2 c.m. from their place of origin. But if the shoot is at a distance of 10 c.m., the roots only develop their root-hairs when they have attained a length of 10 c.m. The rule is, therefore, for the roots to grow until they reach the nutrient soil without developing absorption-cells, and only to provide themselves with them when they are in the earth. It is to be observed that these roots are produced on the suspended shoot at places where, under normal conditions (*i.e.*, if the shoot were not cut off and hung up), no roots would be developed. Subject to abnormal conditions and liable to starvation, the plant sends out these roots for self-preservation.

Phenomena of this kind force one to conclude that a plant discerns places which offer a supply of nutriment, and then throws out anchors for safety to those places. This power of detection may, undoubtedly, be explained by the influence which conditions of moisture, in addition to the action of gravitation, have on the direction taken by growing roots. The root-hairs can only obtain food-salts when the ground is thoroughly moist; and whenever roots, or rather their branches, have to choose between two regions, one of which is dry and the other wet, they invariably turn towards the latter. If seeds of the garden-cress are placed on the face of a wall of clay which is kept moist, the rootlets, after bursting out of the seeds, grow at first downwards, but later they enter the wall in a lateral direction. The longitudinal growth of the roots is greater on the dry side than on the wet side, and this results in a bending of the whole towards the source of moisture, in this instance the damp wall. It has been established that the tip of a rootlet is very sensitive to the presence of moisture in the environment. Where there is a moist stratum on one side and a dry stratum on the other, a root-tip receives a stimulus from the unequal conditions in respect of moisture; the stimulus is propagated to the growing part of the root, which lies behind the tip, and the result is a curvature of the root towards the moist side. Thus, the presence of absorbable nutriment, or rather of moisture, in the ground explains the divergence of roots from the direction prescribed by gravity.

The extent to which the direction taken by roots in their search for food is dependent upon the presence of that food, and the fact that roots grow towards places that afford supplies of nutritious material, are strikingly exhibited, also, by epiphytes growing on the bark of trees, such as tropical orchids and *Bromeliaceæ*; and again by plants parasitic on the branches of trees, of which the Mistletoe and other members of the *Loranthaceæ* afford examples. Although the absorption of food by these plants will not be thoroughly discussed till a later

stage, this is the proper place to mention the fact that in them positive geotropism appears to be completely neutralized. The growing rootlets which spring from the seed, and the absorptive cells produced from minute tubercles, grow upwards if placed on the under surface of a branch, horizontally if placed on the side, and downwards if on the upper surface. Thus, whatever the direction, they grow towards the moist bark which affords them nourishment.

Positive geotropism seems to be quite abolished also in those marsh-plants which live under water. When, for instance, the seed of the Water-chestnut (*Trapa natans*) germinates under water in a pond, the main root emerges first from the little aperture of the nut and begins by growing upwards. Soon the smaller scale-like cotyledon is put forth, whilst the other, which is much larger, remains within the nut. The whole plant so far is standing on its head, as it were, and is growing upwards with its principal root directed towards the surface of the water. Gradually the leafy stem emerges from the bud between the two cotyledons, and likewise curves upwards and grows towards the surface, whilst an abundance of secondary roots is developed at the same time from the main root. Their function is to absorb nutritive substances from the water around, now that the materials for growth stored in the seed are exhausted. Finding an aqueous solution of food-salts everywhere these roots grow in all directions, upwards, downwards, or horizontally to right or left, forwards or backwards, only they carefully avoid touching one another or interfering with each other's sphere of absorption. It is not till much later that the main root changes the direction of its apex and bends downward. New roots are then produced from the stem; but this subject has no further bearing on the problems at present before us.

The movements of roots, as they grow in earth, suggest that they are seeking for nutriment. The root-tip traces, as it progresses, a spiral course, and this revolving motion has been compared to a constant palpitation or feeling. Spots in the earth which are found to be unfavourable to progression are avoided with care. If the root sustains injury, a stimulus is immediately transmitted to the growing part, and the root bends away from the quarter where the wound was inflicted. When the exploring root-tip comes near a spot where water occurs with food-salts in solution, it at once turns in that direction, and, when it reaches the place, develops such absorptive cells as are adapted to the circumstances.

As has been mentioned before, the roots of most land-plants bear root-hairs on a comparatively restricted zone behind the growing point (see fig. 12<sup>3</sup>), and these hairs have only an ephemeral existence. As the root grows and elongates, new hairs arise (always at the same distance behind the tip), whilst the older ones collapse, turn brown, and perish. In ground which contains on every side food-salts in quantities adequate to the demand, and sufficient water to act as solvent and as medium for the transmission of the salts, the absorptive cells are rarely tubular, but exhibit themselves, as already described, in the form of flat cells destitute of outward curvature. This is the case, for instance, with those Alpine plants which grow in

ever-moist hollows and depressions in proximity to springs (e.g. *Saxifraga aizoides* and many others). But wherever the substances to be absorbed are not so easily obtained, the surfaces of the absorptive cells are increased by means of a protrusion of the outer cell-wall, the whole cell being converted into a tube. These tubular absorptive cells are most elongated in mossy forests, where rather large gaps occur not infrequently in the soil. When a root in the course of growth reaches one of these lacunæ, filled with moist air, its root-hairs often lengthen out to an extraordinary extent, and sometimes attain to twice the length of those which are in compact soil. The absorptive cells on the roots of the Water-hemlock (*Cicuta virosa*) and the Sweet Flag (*Acorus Calamus*) do not project at all if the earth in which they grow is muddy; whilst, if the earth is only slightly damp, and an increase of surface is therefore advantageous, the absorptive cells become tubular. Plants which grow in ground liable to periodic drought, and which at these times must secure all the moisture retained by the earth to save their aerial portions from death by desiccation, endeavour to obtain as great an area of absorption as possible by the development of long tubular cells.

The fact must not be overlooked, however, that the form and development of absorptive cells depend partly on the quantity of water that is given off from the aerial parts of the plant, that is to say, by the transpiration of the foliage-leaves. Plants which lose a great deal of water in this way must provide for abundant restitution. They must absorb from as large an area as possible, and enlarge their absorptive surfaces adequately by pushing out the cells into long tubes. For this reason all plants with very thin, delicate, expanded foliage-leaves, which transpire readily and abundantly, have numerous long tubular root-hairs. Examples are afforded by *Viola biflora* and the various species of *Impatiens*. On the other hand, plants with stiff, leathery leaves, being protected by a thick epidermis from excessive transpiration, as, for instance, the Date-palm, exhibit flat, non-protuberant absorptive cells, because there is a very limited amount of evaporation from these plants, and the quantity of water to be absorbed to replace what is lost is therefore small. The same thing holds in the case of evergreen Conifers, in which, owing to the structure of the stiff needles and to the peculiar formation of the wood, water is conducted very slowly from the roots to the transpiring green organs. It has been ascertained that they exhale from six to ten times less vapour than do ashes, birches, maples, and other flat-leaved trees growing on the same ground.

We shall presently return to the question of the substitution for absorptive cells in many coniferous and angiospermic trees and in evergreen *Daphnaceæ*, *Ericaceæ*, *Pyrolaceæ*, *Epacridæcæ*, &c., of the mycelium of fungi, and shall treat also of the importance of the form of the absorptive cells, and of the roots which bear them, in relation to the mechanism of striking root in the ground.

RELATIONS OF THE POSITION OF FOLIAGE-LEAVES TO THAT OF  
ABSORBENT ROOTS.

Anyone who has ever taken refuge from a sudden shower under a tree will remember that the canopy of foliage afforded protection for a considerable time, and that the ground underneath was either not wet at all, or only slightly so. No doubt some of the rain flows down the bark of the trunk, and in many species, as, for instance, the Yew and the Plane-tree, the volume of water conducted down the trunk is considerable; but in the case of most trees the rain-water which reaches the earth in this manner is not abundant, and in comparison with that which drips from the peripheral parts of the foliage its quantity is negligible. This phenomenon is dependent upon the position of the foliage-leaves relatively to the horizon. In almost all our foliage-trees—in limes and birches, apple and pear trees, planes and maples, ashes, horse-chestnuts, poplars, and alders—these organs slope outwards, and are so placed one above the other that rain falling upon a leaf on one of the highest branches flows along the slanting surface to the apex, collects there in drops, and then falls on to a lower leaf whose surface is also inclined outwards. Here it coalesces with the water fallen directly upon this leaf; and so it goes from one tier to another, lower and lower, and at the same time further and further from the axis, till a number of little cascades are formed all round the tree. From the under and outermost leaves of the entire mass of foliage the water falls in great drops to the ground, and after every shower of rain the dry area at the foot of the tree is surrounded by a circular zone of very wet earth. It is only necessary to dig at these places to convince one's self that the tree's absorptive roots penetrate the earth precisely to the wet zone. When a tree is young, its roots lie in a small circle, and the crown too is not extensive, so that the damp zone is proportionately restricted. But as the latter is enlarged there is a corresponding elongation of the roots in their search for moisture, and thus roots and foliage progress *pari passu* in peripheral increase. It seems not improbable that the custom amongst gardeners and foresters of trimming the foliage and roots of trees when the latter are transplanted is to be attributed to the phenomenon above described. For the rule is observed that the branches of the trunk and those of the root must be about equally shortened, and accordingly the suction-roots, as they develop, reach the zone of drip of the growing crown.

A similar method of carrying off water is to be observed in coniferous trees. Take, for example, the Common Pine. The lateral branches are horizontal near the main trunk; the secondary branches curve upwards like bows. The needles near the tip of each of the latter slant obliquely upwards from the axis, whilst the older needles, situated on the under side of the part of the branch which is almost horizontal and at some distance from its extremity, are directed obliquely downwards and outwards. Rain-drops striking the upturned needles glide down them to the bark of the branch in question, and thence to other needles whose

inclination is downwards and outwards. On their apices great drops are gradually formed, which finally detach themselves and fall on to the mass of needles belonging to a lower branch. Thus transmitted, the rain-water travels through the foliage lower and lower and at the same time further from the axis. This is also the case with larches. The drops of rain which fall upon the erect needles of the tufted "short branches" collect and gradually descend to the needles of the drooping "long branches" on lower boughs. Large drops are always to be seen on their drooping apices, whence they drip to the earth. Owing to the pyramidal form of larches, and to the circumstance that the long shoots on each branch are terminal, almost all the water which falls upon one of these trees reaches the long shoots hanging down from the lowest branches, which discharge most of all. Although larches with their tender needles do not look at all as though they would be any protection against rain, the ground underneath them keeps dry nevertheless, the principal part of the water falling upon them being conducted to the periphery. Indeed, the larch belongs to the number of trees which conduct almost all the rain that falls upon them to a certain distance from the axis where the absorbent roots lie, and only allow a little to trickle down the bark of the main trunk.

Many shrubs and perennial herbs also transmit the water, which falls on their upturned laminæ, to parts of the ground where their absorbent roots are embedded; or, rather, the roots send forth their branches bearing absorptive cells to the area which is kept moist by drippings from the leaves. Particularly striking in this respect are the species of the two genera of Aroids *Colocasia* and *Caladium*. A specimen of the latter is figured below (fig. 13<sup>1</sup>). If one digs about individuals of this genus cultivated on open ground, one invariably finds that the tips of the lateral roots, which proceed in a horizontal direction from the bulbous root-stock, are buried under the point of the great leaves which slope obliquely outwards. We must not omit to mention, in addition, that the stalks of leaves which conduct the rain centrifugally are not channelled on the upper surface; they are round, and comparable to wires supporting at their upper extremities the laminæ in an outward and downward direction. As instances we may quote the Horse-chestnut, Maple, and Lime, and many shrubby, suffruticose, and herbaceous plants, such as *Sparmannia*, *Spiraea*, *Aruncus*, and *Corydalis*, and also climbing and trailing plants (e.g. *Menispermum*, *Banisteria*, *Aristolochia*, *Hoya*, *Zanonia*, and *Tropaeolum*). Whenever a system of grooves is developed on the surface of an outward sloping leaf, the channels run along the veins and terminate at the apex of the leaf, or at the apices of the leaf's lobes, and invariably cause the water to travel, not to the basal part, but to a spot on the margin whence it will detach itself in the form of a drop, and fall upon the leaves situated immediately below and at a greater distance from the axis.

A striking contrast to these trees and shrubs, climbing and trailing plants, and suffruticose and herbaceous species, with their absorptive roots lying in one plane, and usually spreading at but little depth, is afforded by plants which possess

bulbs or short root-stocks with deep-reaching suction-roots, and those which have tap-roots descending vertically in continuation of the main stem, and whose secondary roots are short and travel only a little distance from their places of origin. This other extreme in root-structure, which is represented in fig. 13<sup>2</sup>, has its counterpart above-ground in the form and direction of the laminæ upon which the rain falls. In all these plants the surfaces of the leaves are not directed

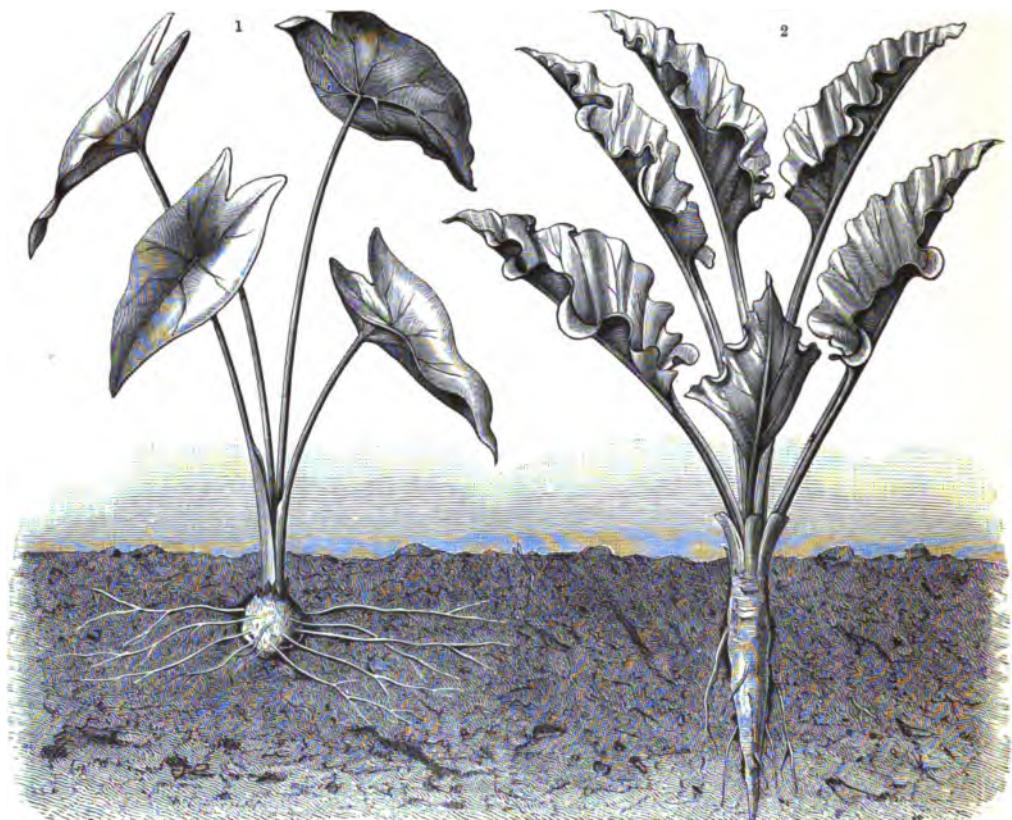


Fig. 13.—Centrifugal and Centripetal Transmission of Water.

<sup>1</sup> By a *Caladium*. <sup>2</sup> By a *Rhubarb* plant.

outwards, but slope obliquely towards the central axis. Their upper sides, moreover, are concave and exhibit a system of grooves, which conveys the water collected by the leaf towards the stem, and therefore also, towards the tap-root and suction-roots. The leaves of bulbous plants, such as the Hyacinth and Tulip, all stand up obliquely, and their upper surfaces are concave and often deeply channelled. Along the grooves the rain flows centripetally downwards, and so directly reaches the part of the earth where the bulbs and suction-roots, which proceed in a tuft from underneath the bulbs, are situated. The young leaves of Cannaceæ and of the Lily-of-the-valley are coiled up like a trumpet; and rain, falling from above upon the expanded portion, is led along the coiled surface, describing a helix as

it goes, to the earth in the neighbourhood of the absorptive roots, which proceed from the short root-stock. When the leaves of plants furnished with tap-roots are arranged in whorls, and are without internodes, and the rosette rests upon the ground, as is the case in the Mandrake, the Dandelion, and several species of Plantain (*Mandragora officinalis*, *Taraxacum officinale*, *Plantago media*), there are always one or more main grooves on the upper surfaces of the leaves, and the leaves have always such form and position as compel the rain which falls upon them to flow centripetally, i.e. towards the tap-root growing vertically beneath the centre. Plants with petiolate leaves, which conduct rain centripetally, always have on the upper side of each leaf-stalk an obvious groove, the depth of which is frequently increased by the development of green or (in many cases) membranous ridges on the two lateral edges. Grooves of this kind are to be seen particularly well on the petioles of the radical leaves of the Rhubarb (see fig. 13<sup>2</sup>), Beet-root, Funkias, and most Violets.

Far more complicated in structure than the radical leaves just described, are caudine leaves. Leaves proceeding from the stem high above the ground, and forming receptacles for rain-water, like those of the Rhubarb, are best fitted to preserve their proper direction when they have no stalks and the base fits directly on to the stem or passes into it. Cup-shaped laminæ, if borne on long erect petioles, necessitate a great expenditure on supporting-cells, and they are, therefore, on the whole, rare. Of the plants we know, only certain Stork's-bills, *Pelargonium zonale*, *P. heterogamum*, &c., afford examples of cup-shaped, caudine leaves of the kind, borne on long, rigid petioles. In most cases, therefore, caudine leaves which conduct water centripetally are either sessile or very shortly petiolate, have their bases close to the stem, and even extend their edges down it more or less in the form of wings and ridges, or surround it in the form of collars, lobes, and auricles, as in the case of so-called amplexicaul leaves.

When the leaves are in pairs opposite one another and the alternate pairs at right angles, an arrangement known as decussate, the surplus water is usually conveyed through two grooves, which run down the intervening piece of stem from one pair of leaves to the next. Each of these grooves begins in an indentation between the margins of the bases of a pair of leaves, and terminates above the midrib of one of the leaves belonging to the next pair. Now, water trickling down such a groove falls precisely on that part of a lower leaf where the rain retained by the surface of that leaf is collected; and so the stream of water becomes more and more copious as it approaches the ground. These grooves may be seen in many species of ringent *Labiatae*, *Scrophulariaceæ*, *Primulaceæ*, *Gentianaceæ*, *Rubiaceæ*, and Willow-herbs; the best-marked instances are found in the Knotty Fig-wort (*Scrophularia nodosa*), the Yellow-rattle (*Rhinanthus*), the meadow-gentians (*Gentiana germanica*, *Rhaetica*, &c.), and the Centaury (*Erythraea*). The grooves always possess the property of being wetted by water, whereas the ungrooved parts of the same stem are not wetted. Sometimes the grooves are fringed with hairs which absorb the water like the threads of a

wick. By means of both contrivances advantage is ensured in that the water only oozes quite gradually down the moistened grooves, or else is conducted by the hairy fringes to the base of the stem, and does not rebound at any spot in the form of drops. Irregularly bounding drops would be liable to fall on the ground at spots where no absorptive organs awaited them.

In cases where foliage-leaves, adapted to a centripetal conduction of rain, are arranged upon a spiral line down the stem, instead of in pairs opposite one another, the water leaks away along the spiral from one leaf to the next, and finally to the bottom. Then, again, there are often grooves in the stem along which the water trickles, as, for instance, in the Common Whortleberry (*Vaccinium Myrtillus*). The erect leaves of this plant conduct the drops as they fall to the branches, which are deeply furrowed. The water travels through the furrows into those of lower branches, and finally along those of the main stem of the whole bush down to the earth. In *Veratrum album* each of the concave caudine leaves has, on the upper surface, a number of deep longitudinal grooves, which all discharge together at the base of the leaf. The water collected there at length overflows and runs down the round stem in no particular channel.

The descent of rain-water along a spiral line may be very clearly traced in many plants of the Thistle tribe. If tiny shot-grains are substituted for rain-drops in a stiff-leaved plant, the course designed for the drops in that particular species may be followed with ease. When strewn on a mature plant of the Safflower (*Carthamus tinctorius*) or of *Alfredia cernua* (fig. 14<sup>1</sup>), the grains of shot roll down the somewhat channelled surface of the highest caudine leaf, which stands up obliquely, and dash against the stem. The latter is half encompassed by the leaf-base, and the shot then roll over one of the basal lobes of the leaf and travel out of the range of that leaf, falling on to the middle of the one next below. For the amplexicaul foliar bases are so placed that each leaf has one of its basal lobes above a concave part of the next lower leaf. In precisely the same way the shot descend from the second leaf to the third, and so on until they reach the earth quite close to the stem. The descent reminds one of the game in which a little ball is made to roll along a spiral groove on to a board furnished with numbered holes. Rain-drops falling upon thistle-like plants of this kind naturally follow the same course as the shot. Only, the additional fact must be taken into account that not only the highest but all the leaves are adapted as receptacles for the rain as it falls, and that consequently the drops falling from leaf to leaf are augmented by new tributaries, and become greater and greater as they descend.

A somewhat different method of water-conduction from that which occurs in the Safflower and in the nodding *Alfredia* is observed in the Milk Thistle (*Silybum Marianum*), in the Cotton Thistle (*Onopordon*), and in the Mullein (*Verbascum phlomoides*). The upper leaves, which have two semi-amplexicaul lobes, are as nearly erect as those of the Safflower and the nodding *Alfredia*, and lead the rain off in exactly the same way. But the leaves in the middle

of the stem are only erect for about three-quarters of their length; the uppermost third, including the apex, is bent obliquely outwards and downwards. Drops of rain falling on this upper third of a leaf would flow in a centrifugal direction, and do, as a matter of fact, drip down from the apex. Now the leaves in all



Fig. 14.—Irrigation of Rain-water.

<sup>1</sup> In *Alfredia cernua*. <sup>2</sup> In a Mullein (*Verbascum phlomoides*).

these plants are shorter the higher their position upon the stem, so that the total contour of the plant may be described as a slender pyramid. In consequence of this, water dropping from the outward-bent and drooping apices of superior leaves is arrested by that part of an inferior leaf which shelves towards the stem, and is thereby conducted centripetally. Thus all the rain-water received by a plant of this kind at last reaches the immediate neighbourhood of the tap-root, and is

a source of nutriment to the absorption-roots which proceed from it. In the Milk Thistle (*Silybum Marianum*) the margins of the caudine leaves are very much waved, and, in consequence of this undulation, three or four depressions exist on each side, through which part of the rain, when there is a heavy downpour, flows off sideways. But even this water, falling laterally, drops upon parts of lower leaves, which conduct centripetally, and so coalesces with the streamlets otherwise produced.

It is very rare for plants which convey water centripetally to have their leaves arranged in two rows. The most striking example of this class is the Japanese *Tricyrtis pilosa*. Its leaves are situated on the fully-developed stem very regularly, one above the other, in two series. Each leaf has two lobes embracing the stem, but the base is fixed somewhat obliquely, so that one of the lobes is fixed higher than the other. Moreover, the higher lobe is closely adpressed to the stem, whilst the lower forms a channel which discharges exactly above the concave surface of the next lower leaf belonging to the other side. When rain falls on this plant, the water, collected by one leaf, flows through the broad exit-channel on to the leaf below on the other side. Thence a somewhat augmented stream falls upon a leaf of the first series, and so on, a peculiar cascade resulting, which falls in a zigzag, from leaf to leaf, until it reaches the bottom, close to the stem.

It would, however, be wrong to suppose that the above explanation sets forth the only significance to be assigned to the various arrangements described. To many plants it is a matter of indifference in what direction rain-water falls from the leaves. Such, for instance, is the case with all marsh-plants with roots buried in mud under water, inasmuch as the rain, as it drops, only goes into the water in the pond or marsh, and could not be conveyed to a definite spot for the sake of the absorbent roots. In the Water-plantain, the Flowering-rush, and the Arrow-head (*Alisma*, *Butomus*, *Sagittaria*), accordingly, no relationship between the form and direction of the leaves and the position of the absorbent roots is to be discovered.

On the other hand, in arundinaceous plants (*Arundo*, *Phragmites*, *Phalaris*) an arrangement has been hit upon which is obviously designed to prevent rain-water from collecting between the haulm and the leaf. As is the general rule with grasses, so also in the above-named kinds of reeds, the stem or haulm is furnished with nodes, and from each node proceeds a leaf the lower part of which encases the haulm in the form of a tube or sheath, whilst the upper part is expanded and presents a flat, strap-shaped or concave surface, standing well away from the stem. The leaves may be folded round the haulm like banners. At the place where the sheath passes into the part of the leaf which stands away from the axis at an obtuse angle, one observes on the edge of the leaf close to the angle, two distinct depressions which represent conduits and convey part of the rain from the lamina. There is also a very neat contrivance here in the form of an erect dry membrane which acts as a dam, the so-called "ligule." This membrane, inserted upon the leaf-sheath, is, like the sheath, in contact with the haulm. When rain-

water flows down to this place it is stemmed by the membrane, as by a dam, and diverted right and left into the two grooves. In this way water is prevented from accumulating between the leaf-sheath and haulm, where it might do damage. In many reeds the contrivances for irrigation are even more complete than this. Sometimes hairs depend from the margin of the membrane in the direction of the grooves and, like a wick, lead the water in the proper direction.

An opportunity will occur later on of showing how the conduction of rain to particular spots has an important bearing on the phenomenon of absorption by aerial parts of plants: and also in the regulation of transpiration; and how, by means of the apparatus for water-irrigation, not only absorptive cells at the extremities of roots in the earth, but special organs on the foliage-leaves as well, are often supplied with water.

---

### 3. ABSORPTION OF ORGANIC MATTER FROM DECAYING PLANTS AND ANIMALS.

Saprophytes and their relation to decaying bodies.—Saprophytes in water, on the bark of trees, and on rocks.—Saprophytes in the humus of woods, meadows, and moors.—Special relations between Saprophytes and the nutrient substratum.—Plants with traps or pitfalls for animals.—Insectivorous plants which perform movements for the capture of prey.—Insectivorous plants with adhesive apparatus.

#### SAPROPHYTES AND THEIR RELATION TO DECAYING BODIES.

Whenever plants which take up organic compounds formed in the process of decay are the subject of discussion, the first examples that occur to everyone are members of the great family of Fungi, specimens of which make their appearance wherever dead animals or plants are undergoing decomposition. We recall the moulds, plasmodia, puff-balls, and mushrooms, which grow from dead organic bodies, and are associated with the unpleasant mouldy and cadaverous smell always perceptible in their neighbourhood.

Many of these organisms do, in fact, belong to the class of Saprophytes. Indeed, one group of them is itself the cause of the chemical decomposition of dead plants and animals called decay. Their elongated thin-walled cells, the so-called "hyphæ", thread themselves through dead bodies, and unite to form strands, bundles, networks, and membranes, the whole constituting a structure to which the term "mycelium" is applied. These mycelia are often to be seen, with the naked eye, covering large areas. For instance, in damp cellars, mines, and railway-tunnels, any old rotten wood-work is clothed with delicate, whitish reticula and membranes. The heaps of grape-skins, stalks, and other refuse piled up in the open air by the side of vineyards after a vintage, are usually so completely overgrown by mycelia

that their colour is quite altered. The so-called "mushroom-spawn", used in the cultivation of mushrooms, is also nothing but a mycelium, which entirely invests the manure employed in the cultivation of that fungus, and gives it a white mottled appearance.

In addition to Fungi, however, a number of Mosses, Liverworts, Ferns, Lycopods, and Phanerogams take up organic compounds from the products of decay to serve as their food.

In deciding whether a plant takes up only the mineral substances rendered soluble by the decomposition of the soil, or only organic substances disengaged by the decay of dead plants and animals, we depend generally on the condition and appearance of the nutrient substratum, and, in particular, on its composition, i.e. whether it is exclusively or predominantly organic. But such observations give a very uncertain indication. For, on the one hand, it is possible for plants rooted in a substratum of decaying matter to take nothing but mineral salts (i.e. inorganic compounds) from it; and, on the other hand, it frequently happens that sand or clay, apparently uncontaminated with organic matter, is saturated by water which oozes from a layer of humus in the vicinity, and brings with it organic compounds in solution. The following facts are instructive with reference to the former of these two phenomena. Maize, barley, and other cereals may be reared in fluids, so prepared as to contain a small quantity of mineral food-salts dissolved in distilled water (12 mg. potassium phosphate, 12 mg. sodium phosphate, 27 mg. calcium chloride, 40 mg. potassium chloride, 20 mg. magnesium sulphate, 10 mg. ammonium sulphate, and a few drops of iron chloride in a litre of distilled water), all organic compounds being carefully excluded. When the plants germinate, they develop roots which descend in the liquid and absorb from it mineral salts according to their requirements. They produce stems, leaves, flowers, and, ultimately, seeds capable of germination. Other plants of maize or barley reared simultaneously in richly-manured ground develop likewise leaves, flowers, and fruit. Moreover, analysis of the ash in both cases reveals the fact that the plants which took their nutriment from the manure contain the same salts as those reared in the made-up solution of salts free from organic compounds. Hence, the conclusion may be drawn that a plant of this kind is capable of obtaining an adequate supply of food-salts equally well, either from earth free from humus and manure, or from humus or manure themselves. The experiment further shows that, in the latter case, organic compounds need not necessarily be absorbed, in addition to the mineral constituents of humus or manure which are disengaged during decomposition.

We must next refer to a fact in connection with the second point above mentioned, viz. that plants rooted in sand or loam devoid of humus may yet have organic compounds brought to them by water filtering through a stratum of humus near at hand. The fact in question is, that the very water which one would least expect should contain organic compounds, that, for instance, of cold mountain streams, does very generally include traces of such compounds. On looking through analyses of mineral springs, one finds for the most part, amongst their constituents,

combustible bodies arising from the dissolution of organic matter. Even the acid formerly designated by Berzelius by the name of "spring-acid", is doubtless a product of the decay of fragments of plants in the place where the water of the spring collects. So also is humic acid, a compound produced by decay. The nature of this acid is not yet, it is true, thoroughly known, and it may be a mixture of several acids. We know, however, that it is easily soluble in water, and that it forms soluble compounds with alkalies. Brooks running through woods or meadows, small mountain lakes adjoining peat-beds, and pools in actual peat, consist of water, brown in colour, which gives an acid reaction, and contains invariably organic substances in solution.

The following observations are of great interest in connection with this subject. In the salt-mine at Hallstatt (Upper Austria) one of the galleries, which is hewn through rock and contains no wood-work of any kind, exhibited (spread out upon its smooth limestone roof) the mycelium of a fungus (an *Omphalia*), which certainly required organic nutriment. There were no decaying animal or vegetable remains anywhere in the gallery, and the mycelium derived nourishment solely from water oozing from above through a few narrow cracks in the stone whereby the surface of the latter was kept moist. This water came from a meadow lying high above the mine. Between the two was a thick stratum of limestone with a deep layer of earth resting upon it. The water was clear and colourless, and contained a certain amount of lime, but no perceptible trace of organic substances. Yet this water must have brought organic matter from the meadow above into the mine, and the minute quantity so introduced sufficed to enable the fungus mycelium to grow luxuriantly.

In the Volderthal, near Hall, in Tyrol, there is a spring of cold clear water rising out of slate at a height of 1000 metres above the sea-level, which is filled at its source with a dark thick felt. The felt may be lifted out in pieces the size of one's hand, and it is the mycelium of a fungus, probably a *Peziza*. It clings to slabs of slate, between which the water trickles abundantly, and its nutriment can only be derived from this water. There are pine-woods and meadows in the neighbourhood, but no greater amount of vegetation, humus, or rotten timber than is found near other springs.

These instances satisfactorily prove that even the clearest mountain springs contain organic substances in quantities sufficient, however minute, to nourish fungi. When the origin of springs is taken into account, this result is not really surprising. They are fed by deposition from the atmosphere. The water thus deposited percolates into the ground, passing, in the first place, through a layer of earth-mould which is covered by vegetation, and contains more or less humus in its upper strata. A small quantity of the products of decay is inevitably absorbed, and even if they are partially withdrawn again in lower strata of the earth, traces are still retained by the water in its descent to greater depths, and re-ascent to the surface in the form of springs. The characteristics of the great veins of water which ascend in this way are no doubt common to the smaller veins which originate

in the vegetable mould saturated by snow and rain on the ground of forests or in the humus covering meadows, and which percolate through into the sand or loam beneath. Plants whose roots ramify in this deeper layer of earth derive thence the organic compounds conveyed by the water, and have the additional advantage of being able to satisfy at the same time their requirements as regards mineral substances. This circumstance is of importance not only to flowering-plants but also to many fungi, as, for instance, to all species of *Phallus*, they having need of a great deal of lime. An explanation is thus afforded of the fact, formerly difficult to understand, that in forests and meadows not only the upper black or brown humus layer, but also the underlying yellow loam, or pale sand, neither of which latter contains any humus, has mycelia of fungi running through it in every direction, and weaving their threads over little fragments of rock. Indeed, it sometimes happens that the lower layer of earth is more abundantly penetrated with plexuses of hyphæ than is the upper layer, consisting of vegetable mould. The greatest number of saprophytes is to be found therefore at places where the humus layer is not too thick and loam or sand occurs at no great depth; but where decaying vegetable remains are piled metres high, as on moors, for example, instead of fungi being produced in extraordinary abundance, as one might expect, only a few occur. Pure peat is by no means a favourable soil for fungi, a circumstance which may be partly due to the antiseptic action of certain compounds developed in it.

It follows from the foregoing observations that a sure conclusion as to the nature of plants rooted in a particular substratum cannot possibly be derived from the mere appearance of the substratum. Moreover, the conditions necessary for the growth of plants requiring organic products of decay as nutriment appear to be of much wider occurrence than one would suppose upon a cursory observation of the conditions existing in fields and forests, or, if one considers exclusively instances of cultivated plants reared on arable land, which is manured and constantly turned over. The great variety of plants produced on a limited area is also now intelligible. From the same soil some absorb organic compounds, others mineral substances only; whilst others again take some organic and some mineral food-salts. The determining factor is not the amount of a given substance present in the substratum, but rather the special needs of each species, and ultimately the specific constitution of the protoplasm in each one of the plants which thus, side by side, nourish themselves in totally different ways.

If, then, neither the appearance of the ground nor its richness in respect of humus affords any certain indication as to whether a particular plant lives on organic products of decay or not, the question may perhaps be solved by the fact of the plant's containing or not containing green chlorophyll-corpuscles. We may take it as proved by many results of investigation, that the decomposition of the carbon-dioxide absorbed by a plant from the air, and the formation of the organic compounds of carbon, hydrogen, and oxygen known as carbohydrates (which play so important a part in vegetable economy), only take place in organs possessing the green pigment known as chlorophyll. We shall return to a discussion of these

processes in detail later on, but the fact must be taken into consideration here. One would suppose, accordingly, that plants able to obtain ready-made organic compounds from a nutrient substratum could spare themselves the trouble of building them up, so that the presence of chlorophyll would be superfluous. This conjecture is in fact supported by the absence of chlorophyll in fungi, which are typical instances of saprophytes. But, on the other hand, some plants appear to negative this assumption, or at any rate to deprive it of general application. In mountain districts, where cattle continually pass to and from the meadows and alps, one notices on their halting grounds, and along their tracks, moss of a conspicuous green colour growing on circumscribed spots. On closer examination we find that we have here an example of the remarkable group of the *Splachnaceæ*, and that it has selected the cow-dung to be its nutrient substratum. Each growth of emerald green, *Splachnum ampullaceum*, is strictly limited to the area of a lump of dung; no trace of it is to be seen elsewhere. All the stages of development of this moss follow one another upon the same substratum. First of all the lumps of dirt which are kept moist by rain or by standing water, become enveloped in a web of protonemæ, and their surfaces acquire thereby a characteristic greenish lustre. Later, hundreds of little green stems, thickly clothed with leaves, emerge, and the spore-cases, which resemble tiny antique jars, and are amongst the prettiest exhibited by the world of mosses, become visible as well. Just as *Splachnum ampullaceum* is produced on the dung of cattle, so is *Tetraplodon angustatus* on that of carnivorous animals, and there can be no doubt that these, and in general all *Splachnaceæ*, are true saprophytes. A similar remark holds with regard to the green *Euglenæ* which escape from Hormidium-cells, and fill the foul-smelling liquor in dung-pits and puddles near cattle-stalls in mountain villages, and which multiply to such an extent that in a few days the liquid changes colour from brown to green.

Thus plants do exist containing chlorophyll although absorbing from the substratum organic compounds alone, and containing it, indeed, in such quantities that its presence cannot be looked upon as accidental. It follows, firstly, that absence of chlorophyll is not the distinguishing mark of saprophytic plants; and, secondly, that the organic nutriment of the plants above mentioned cannot be used forthwith unaltered in the building up and extension of their structures, but, like inorganic material, must undergo various changes, that is, must be to a certain extent digested before being used for construction. The probability is that green saprophytes take carbon from their substratum in a form unfitted for the manufacture of cellulose and other carbohydrates. Saprophytes that are not green must obtain carbon from the substratum in the form of a compound, the direct absorption of which could be dispensed with if chlorophyll were present; but it does not necessarily follow that all the organic compounds absorbed by non-green saprophytes are capable of immediate service as materials for construction without any preliminary alteration.

Impartial consideration of the above facts forces us to conclude that there is no

well-marked boundary line between plants which absorb organic compounds and those which absorb inorganic compounds from their respective substrata; and that there undoubtedly exist plants capable of taking up both kinds of material at the same time. This conviction is strengthened still further by the circumstance, which has been repeatedly confirmed by experiment, that plants susceptible of being successfully reared in artificial solutions of mineral salts—to the exclusion of organic compounds—do not entirely reject organic compounds when the latter are tendered to them, but unquestionably assimilate some of them (urea, uric acid, glycocoll, &c.) and work them up into constituents of their own frames.

But, in spite of the impossibility of drawing a sharp line of demarcation between the two groups, it is convenient to treat of the absorption of organic compounds separately, because this division of the subject affords the best opportunity of inspecting in detail, and of surveying generally, the conditions of food-absorption, the comprehension of which is otherwise difficult. In order to determine in each individual case whether a given plant lives either exclusively or principally upon organic food, derived from decaying animal or vegetable remains, reliance must be placed on experiments with cultures; and, in the absence of better vantage-ground, the results of the rougher experiments made by gardeners should not be neglected, always providing that they are accepted subject to possible correction by subsequent exact experiment.

#### SAPROPHYTES IN WATER, ON THE BARK OF TREES, AND ON ROCKS.

Of the special cases of absorption of organic compounds from decaying bodies, we have first of all to consider those occurring amongst water-plants. In the sea, wherever there is an abundance of animal and vegetable life there is also plenty of refuse, for there death and decay hold a rich harvest. The quantity of organic matter dissolved in the water is naturally greater in these places than where vegetation and animal life are less conspicuous. There is a much more varied flora and fauna to be met with in the sea near its coasts, especially in shallow inlets, than at a greater distance from the shore; and the number of dead organisms is also greater near the coast. A mass of organic remains is thrown up by the tide, and by waves in stormy weather. This mass rots during the ebb. Part of it is dragged out to sea again by the next high tide, and then flung up once more; so that the beach is always strewn with dead remains, and the sea near the shore contains more products of decomposition than in the open.

In the immediate neighbourhood of seaports, moreover, or wherever people live, the volume of refuse is considerably increased, and the water in harbours and stagnant inlets behind breakwaters, and at the mouths of canals and sewers, contains such a large quantity of organic refuse in a state of decomposition that its presence is revealed by the odour emitted. Now it is just at these places that an abundant vegetation of hydrophytes is developed. Not only the bottom of shallows, but stones, stakes, quays, buoys, and even the keels and planks of boats long anchored

in harbour, are overgrown by *Ulva*, wracks, filamentous algae, and *Florideæ*. Not a few, as, for instance, the so-called sea-lettuce (*Ulva lactuca*), several species of *Gelidium*, *Bangia*, and *Ceramium*, and the great *Cystosira barbata*, thrive best and in greatest abundance in polluted water of the kind; and there can be no doubt that this is to be accounted for by the presence of a greater quantity of organic compounds in that water.

It is not only in contaminated sea-water, but also in other collections of water which contain products of putrefaction in solution, that we find a characteristic vegetation. We have already alluded to the presence of *Euglena* in the liquor of manure-pits. They occur also at the foot of shady walls, in dirty back streets in towns, in the puddles, and on ground which is saturated with urine and impurities of every kind. These places are the home of a number of other minute plants, which stain the polluted ground after rain with the gayest colours. There, side by side with black patches of *Oscillaria antliaria* and verdigris-coloured films of *Oscillaria tenuis*, are blood-red patches of *Palmella cruenta*, and brick-red patches of *Chroococcus cinnamomeus*. Equally characteristic is the vegetation which covers the earth at the mouths of drains, and is bathed by the trickling sewage. Large areas here are overgrown by the green *Hormidium murale*, which weaves itself over the mire, and by the dark, actively-oscillating *Oscillaria limosa*; and, above all, the curious *Beggiatoa versatilis* makes itself conspicuous, sending out from a whitish gelatinous ground mass long oscillating filaments, which emerge after sundown, and next day split up into innumerable little bacteria-rods. The red-snow alga, too (represented in Plate I.), lives at the expense of the pollen-grains, bodies of insects, and other decaying matter blown on to snow-fields; whilst the nearly allied blood-red alga (*Hæmatococcus pluvialis* or *Sphaerella pluvialis*) lives in the water in hollow stones where all sorts of animal and vegetable remains collect. Leaves blown into deep pools, and lying rotting at the bottom, are everywhere overgrown by green *Edogonium*, by *Pleurococcus angulosus*, and by the amethyst-coloured *Protococcus roseo-persicus*. The bottoms of ditches on peat-bogs, which are full of brownish water containing an abundance of compounds of humic acid in solution, are covered with this amethyst *Protococcus*, whilst a profusion of small filamentous algae, *Oscillariæ* and so forth (*Bulbochaete parvula*, *Schizochlamys gelatinosa*, *Sphaerozoisma vertebrata*, *Microcystis ichthyloba*, &c.), as well as a group of dusky mosses (*Hypnum giganteum*, *H. sarmentosum*, *H. cordifolium*), all have their home exclusively in still water richly supplied with organic compounds. When we include also the curious mould-like *Saprolegniæ* produced on dead bodies floating in water—*Saprolegnia ferax* and *Achlya prolifera* on flies and fishes—some idea is obtained of the great variety of saprophytes living in fresh water, as well as of those inhabiting the sea.

A much more agreeable and attractive picture than that of these aquatic saprophytes is afforded by plants whose sole habitat is the bark of trees. The dead bark does not constitute the nutrient base of all the plants which grow from trunks and branches, or climb up them in the form of clinging and twining lianas.

Often the trees only serve as supports, by means of which the plants in question raise themselves out of darkness into light. Such food-salts as they require they take, not from their support, but from the earth, into which they send absorptive roots. As years go by, a quantity of inorganic dust collects in the forks of branches and in the little rents and fissures in the bark of old trees, and this dust gets mixed with crumbled particles of bark. The clefts, therefore, are more or less full of vegetable mould, and this forms an excellent foster-soil for a large number of plants. But it is not necessarily the case that all plants rooting in this mould take up organic compounds from it. Thus, one finds not infrequently in the angles of bifurcation of the trunks of old limes and other trees, little gooseberry and elder bushes, and bitter-sweet plants, which have germinated there from fruits brought by black-birds, thrushes, and other frugivora. These shrubs, in the forks of limes and poplars hardly take any organic compounds from the mould in which they are rooted, but confine themselves to the absorption of such mineral salts as they may require.

But, with the exception of instances of that kind, the great majority of plants, nestling in the mould in crevices of bark, do take nutriment from this their substratum in the form of organic compounds. In cold regions the plants living in the mould of bark are for the most part mosses and liverworts. They cover trunks and branches of old ashes, poplars, and oaks, with a thick green mantle, and grow especially on the weather-side of the trees. In the tropics, on the other hand, the fissured bark of trees is a rallying ground not only for delicate mosses and moss-like *Lycopodia*, but also for a whole host of ferns and vivid flowering plants. The number of small ferns which develop and unroll their fronds from chinks in the bark of trees is so great that old trunks appear wrapped in a regular foliage of fern-fronds. Of Phanerogams, in particular, the *Aroidæ*, *Orchidaceæ*, *Bromeliaceæ*, *Dorsteniæ*, *Begoniaceæ*, and even *Cactaceæ* (species of the genera *Cereus* and *Rhipsalis*) bury their roots in the mould of bark. It is to be remarked that the rosettes of *Bromeliaceæ* ornament chiefly the forks of trunks, whilst *Dorsteniæ*, *Orchideæ*, and the various species of *Rhipsalis* grow on the upper side of branches that ramify horizontally; whilst, lastly, *Aroidæ* and *Begoniæ* take root, for the most part, on the surfaces of huge erect trunks.

Besides the mould collected in crevices and fissures of bark, the bark itself, that is, the cortical layer, dead but not yet crumbled and mouldered into dust, forms a nutrient substratum for a whole series of plants of most various affinity. Many fungi and lichens penetrate deeply the compact bark, and their hyphal filaments ramify between its dead cells. Other plants, instead of piercing through the substance of the bark, lay themselves flat upon its surface, and grow to it so firmly that if one tries to lift them away from the substratum, either part of the latter breaks off, or the adnate cell-strata are rent, but there is no separation of the one from the other. If a tuft of moss (e.g. *Orthotrichum fallax*, *O. tenellum*, or *O. pallens*), growing on bark, or a liverwort (e.g. *Frullania dilatata*) closely adherent to a similar basis, is forcibly removed, little fragments of the bark may be

always seen torn off with the rhizoids at the places where they issue from the stemlets. The same thing occurs in the case of the roots of tropical orchids growing to the tree-trunks which constitute their habitat. The majority of these tree-orchids nestle, no doubt, in mould-filled crevices of the bark, and nourish them-



Fig. 16.—Aerial Roots of a Tropical Orchid (*Sarcophyllum rostratum*) assuming the form of straps.

selves, besides, by means of special aerial roots which hang down in white ropes and threads, like a mane, from the places where the plants are situated upon the trees, and which will presently be described in detail. But a small section develops strap-shaped roots as well, which adhere firmly to the bark with their flat surfaces. This phenomenon is most strikingly exhibited by the splendid *Phalaenopsis*

*Schilleriana*, a native of the Philippine Islands; its roots are rigid, compressed, and about 1 c.m. in breadth; the surface turned away from the trunk is slightly convex, and has a granular structure and metallic glitter like a lizard's or chameleon's tail. The surface towards the trunk is flat and without metallic glitter, and upon it, close behind the growing point, there is a whitish fur consisting of short, thickly packed, absorptive cells. When the tip of one of these roots comes into contact with the bark it grows so firmly to the substratum by means of the absorption-cells, that it is easier to detach superficial bits of the bark itself than the root. The latter, once fixed, flattens out still more and becomes strap-shaped, whilst creeping outgrowths proceed from it, forming strips which may ultimately attain a length of 1½ metres. The sight of a trunk covered with these long metallic bands is one that never fails to excite wonder even in the midst of the world of orchids, wherein, as is well known, there is much to marvel at.

In other species of tropical orchids, e.g. in *Sarcanthus rostratus* (fig. 15), the roots are not flat from the beginning, but become so when they come into contact with the bark. A root is often to be seen which arises as a cylindrical cord from the axis, then lays itself upon the bark in the form of a band, and further on lifts itself once more, resuming at the same time the rope form, as is shown in the illustration. Here also complete coalescence takes place between the bands and the bark, and the union is extremely close. Similar conditions have been observed to hold in many *Aroideæ* living on the bark of trees. The plants in question lie with their stems, leaves, and roots flat against the trunks, so that they suggest a covering of drapery. Taking, for instance, the *Marcgraviæ* (*Marcgravia paradoxa*, *M. umbellata*), one might at first sight suppose that they adhere to the bark not only by the roots, but also by the large discoid leaves, which are arranged in two rows. A very remarkable fact also, in connection with these plants, is that they only grow on very smooth and firm bark. When transferred to a soft substratum, such as mould or moss, they languish, because their roots are unable to enter into close union with a support of such loose texture. This is also true of most tropical orchids living on bark. When their seeds are transferred to loose earth devoid of humus, they do indeed germinate, but then perish, whereas when sown on the bark of a tree, they not only germinate, but grow up with ease into hardy plants.

Where steep rocks occur near clumps of trees it is not uncommon for the same species of plants to grow on both. Allusion is not here made to kinds which, like ivy, have their roots in the earth at the foot of rocks and trees, and creep up the one or the other indifferently, using both merely for support and not as sources of nutriment, and clinging to them by means of special attachment-roots. The remark is applicable also to plants which live on the products of the decay of organic bodies, for example many tropical *Orchideæ*, *Dorstenieæ*, *Begonieæ*, and Ferns; and in cooler parts a number of Mosses and Liverworts. It is not difficult to explain this phenomenon in the case of species which derive their food from vegetable mould. The crannied wall of rock is, in a certain way, analogous to the rugged bark of a tree. The holes in the rock are filled in course of time with black vegetable mould,

and plants with foliage, flowers, and fruit of a form adaptable to cracks and holes are able to establish themselves in the mould there, just as well as in that collected in crevices of bark. In one respect, indeed, they are even more favourably situated. For the humus in bark gets quite dry in long periods of drought, because no water is yielded to the bark by the wood of a tree, even though the latter be abundantly supplied with sap; whereas, in the case of rocks the probability is, the clefts being very deep, that even when the top layers of humus filling them yield up their water to the air, a certain restitution of moisture takes place from the deeper parts, which are never quite dry. Moreover, plants growing in the mould of rock crevices are able to send their roots down to much deeper strata than is possible in the case of bark. This is another reason why deep cracks in rocks, filled with humus, exhibit a richer flora, as a rule, than do the much shallower crevices in the bark of trees, although, as has been said before, the two habitats have many plants in common.

It is more difficult to explain how it happens that plants which derive their sustenance, not from the mould in crevices, but from the substance of the bark itself, and which lie flat against its surface, are also found adhering to walls of rock. As an example take *Frullania tamarisci*, a Liverwort with small brown bifurcating stems, which bear double rows of leaves and are of dendritic appearance. This plant grows equally well on the bark of pines or on the face of adjacent gneiss rocks. At first sight it would seem scarcely possible that a plant of this kind, clinging to the unfissured surface of rock, should be in a position to obtain organic compounds from its substratum. This is nevertheless the case. Closer inspection reveals the fact that the Liverwort does not adhere to blank rock, but to a part formerly clothed by rock-lichens. This inconspicuous incrustation of dead lichens is a complete substitute for the superficial layer of bark, and it is into it that the *Frullania tamarisci* sinks its roots. Another way by which food is supplied to plants adherent, like the above, to vertical and unfissured rocks will be discussed later on.

#### SAPROPHYTES IN THE HUMUS OF WOODS, MEADOWS, AND MOORS.

Damp shady woods, especially pine woods, are particularly well furnished with saprophytes. Here again we find representatives of the same families as choose the bark of trees for their habitat. On the ground of woods, the most characteristic forms are mosses, fungi, lycopods, ferns, aroids, and orchids. The dark-brown humus, produced from dropped and decaying needles, is first of all covered by a rich carpet of mosses, such as the widely distributed *Hylocomium splendens*, *Hypnum triquetrum*, and *Hypnum Crista-castrensis*. The mouldered dust of dead trees has a clothing of *Tetraphis pellucida* and of *Webera nutans*, and decaying trunks are overgrown by the cushions of species of *Dicranum* (*Dicranum scoparium*, *D. congestum*, *Dicranodontium longirostre*), pale feathery mosses (*Hypnum uncinatum* and *H. reptile*) and various liverworts. Everywhere above the soft, ever-moist carpet of moss rise green fronds belonging to broad-leaved ferns.

Woods are also the special abode of fungi, and the damp ground is covered towards autumn by innumerable quantities of their curious fructifications. Dropped needles and cones, leaves and sticks strewn upon the ground, fallen trunks, and even the dark amorphous dust arising from the mouldering of these bodies and of the numerous roots ramifying in the ground, appear to be perforated by and wrapped in the protoplasmic threads of plasmoid fungi, or similarly invested by a plexus of filaments, the so-called mycelia of other forms of fungi. Amongst the scaly fragments of bark, peeling from the trees, they appear in the form of slimy strings, or as a dark trellis and net-work, inserted between the bark and wood of the rotting tree; on the stripped white trunk they are in dark zigzag lines like those of forked lightning; and between, the white mycelia of huge toadstools and tremellas are woven in all directions. Here and there large areas of the brown decaying soil are flecked and speckled by these mycelia, and even the dead stems of the mosses on the ground are festooned with white fleece, and wrapped round by hyphæ.

It is worth while to glance too at the reciprocal relations of these woodland plants. We find mosses, lycopods, and various ferns and phanerogams living upon the fallen twigs and needles, and on the mouldering roots of pines and fir-trees. The dead remains of those plants afford sustenance to the fungi, which lift their fructification above the bed of moss. In their turn the rotting fructifications of the larger fungi form a nutrient substratum for smaller fungi, which cover the decaying caps and stalks with a dark-green velvet. Lastly, these little fungi, too, fall a prey to corrupting bacteria, and are resolved into the same simple inorganic compounds as were absorbed from the air and earth, in the first instance, by the pines and fir-trees. In the depths of forests there is going on, for the most part unseen by us, a mysterious stir and strife, accompanied by an uninterrupted process of exchange between the living and the dead, and a marvellous transformation of those very substances whose secret we have only partially succeeded in solving.

The results of cultivation have proved that in the group of flowering-plants belonging to the woodlands of Central and Northern Europe, which derive sustenance partially or entirely from the organic compounds afforded by the humus, are to be included, amongst others, the various species of coral-wort (*Dentaria bulbifera*, *D. digitata*, *D. enneaphyllos*), *Circeea alpina*, *Galium rotundifolium*, and *Linnaea borealis*, and above all a large number of orchids. Of these, *Dentaria* prefers mould produced from the beech leaves, and *Circeea*, *Galium*, and *Linnaea* appertain to the mould of pine-woods. Of the orchids some are provided with green leaves, as, for instance, the delicate little *Listera cordata*, *Goodyera repens* remarkable for its villous petals, and the various species of *Cephalanthera*, *Epipactis*, and *Platanthera*; others, such as *Limodorum abortivum*, the bird's-nest orchis, the coral-root, and *Epipogium aphyllum* have none. *Limodorum abortivum* belongs rather to the warmer districts of Central Europe. It has fleshy root-fibres, twisted and twined into an inextricable ball, and a slender steel-blue stem, over half a metre in height, bearing a lax spike of fairly large flowers, which

subsequently become paler in colour. The bird's-nest orchis (*Neottia Nidus-avis*) is of wide distribution both in forests of pines and in those composed of angiospermous trees. Its stem and flowers are of a light-brown colour, unusual in plants, but somewhat like that of oak-wood. The flowers have no scent, and the numerous roots, issuing from the subterranean part of the stem and imbedded in humus, remind one in form and colour of earth-worms, and together constitute a strange tangled mass as large as a fist. The latter has been thought to resemble a bird's nest, and to this is due the name of the plant. The coral-root (*Corallorrhiza innata*), unlike the bird's-nest orchis, has no root at all; but, on the other hand, the subterranean portion of the stem, the so-called rhizome, possesses a distant resemblance to the root-tangle of *Neottia*. Pale-brownish branches of this rhizome, which bifurcate repeatedly at their obtuse and whitish extremities, looking as if they had been subjected to pressure for a time, and all the short lobe-shaped branchlets thereby spread out into one plane, lie closely crowded together, sometimes crossing one another, and so form a body which vividly recalls the appearance of a piece of coral. This underground coral-like stem-structure develops each year pale greenish shoots which rise above the ground and bear small flowers speckled with yellow, white, and violet, and exhaling a scent of vanilla; later, green fruits of a comparatively large size develop, turning brown when they ripen.

The fourth mentioned of these pale wood-orchids, the *Epipogium aphyllum*, is at once the rarest and most curious of them all. Like the coral-root it has no true roots. Its rhizome so closely resembles the latter's that it is easy to mistake the one for the other; but they may be distinguished by the fact that in the case of *Epipogium* the rhizome sends out long filiform shoots, which swell up like tubers at their tips, and may be regarded as subterranean runners. The swollen extremity becomes the point of origin of a new coral-like structure, which develops at about the distance of a span from the old one; whilst the latter, usually exhausted after flowering, gradually perishes. This coral-like stem lives of course underground, and is not visible till one lifts away the moss from the mould on the ground. It is often completely imbedded in sandy loam, lying immediately beneath the black mould. Many years frequently go by without the *Epipogium* producing flowers. The plant meanwhile lives entirely underground. In the course of a summer in which it has not flowered, anyone not having previous exact knowledge of its whereabouts might pass by without dreaming that the bed of moss and humus on his path concealed this strange growth. The flowering stems which at length emerge, when there is a warm summer, are right above the place where they branch off from the subterranean rhizome. They are thickened in a fusiform manner, and have, for the most part on one side, a reddish or purplish tinge. Everything connected with them is tense, smooth, full of sap, and almost opalescent. The few flowers that are borne by the stem are comparatively large, and emit a strong perfume resembling that of the Brazilian genus of orchids *Stanhopea*. The colouring, too, a dull yellowish white with touches of pale red and violet, reminds one of these tropical orchids.

The sight of the pale-coloured plants lifting their heads, at flowering time, from the tumid carpet of moss has all the stranger effect because, as a rule, no other flowering plants are visible in any direction. The flowers are suspended by delicate drooping pedicels, and owing to their peculiar colour, fleshy consistence, and form—the erect concave petal like a Phrygian cap or helmet, and the others stretched out like prehensile limbs—remind one of the opalescent medusæ which float on the blue sea waves. The propriety of the analogy is enhanced by the fact that the form and colour of other saprophytes produced near *Epipogium* in woods have a striking resemblance to the animals and wracks which inhabit the sea-bottom. The fungi, known by the name of club-tops, much-branched, flesh-coloured, yellow or white *Clavariae*, which often adorn whole tracts of ground in a wood, imitate the structure of corals; *Hydnææ* are like sea-urchins, and *Geaster* like a star-fish, whilst the various species of *Tremella*, *Exidia*, and *Guepinia*, which are flesh-pink, orange, or brownish in colour, and the white translucent *Tremellodon gelatinosum*, resemble gelatinous sponges. The small stiff toad-stools (*Marasmius*), which raise their slender stalks on fallen pine-needles, remind one of the rigid *Acetabulariae*. Other toad-stools, with flat or convex caps exhibiting concentric bands and stripes, such as the different species of *Craterellus*, have an appearance similar to the salt-water alga known by the name of *Padina*. Dark species of *Geoglossum* imitate the brown *Fucoideæ*; and one may fancy the red warts of *Lycogala Epidendron*, a plasmoid fungus inhabiting the rotten wood of dead weather-beaten trees, to be red sea-anemones with their tentacles drawn in, clinging to gray rocks. However far-fetched this comparison between the two localities may seem at first sight, everyone who has had an opportunity of thoroughly observing the characteristic forms of vegetable and animal life in woods, and at the bottom of the sea, will inevitably be convinced of its accuracy.

Meadow-land, rich in humus, is much more sparsely occupied by saprophytes than the soil of woods. There is no lack of the strange forms of toad-stools and puff-balls, whose fructifications often spring up in thousands, especially in the autumn, in company with the meadow-saffron; but in numbers they are not to be compared with those which occur in the mould of woods. Amongst ferns and phanerogams, the following species are dependent upon the organic compounds arising from the decomposition of the humus: Moonwort (*Botrychium Lunaria*), numerous orchids, blue and violet-flowered gentians, the famous *Arnica*, Polygalaceæ, and more especially several grasses, chiefly the Matweed (*Nardus stricta*) which, when once it has struck root in the humus, extends in dense masses over large areas. Several plants, too, adorning alpine pastures, and belonging for the most part to the same families as the species mentioned above, are to be regarded as humus-plants. Such are the Alpine Club-moss (*Lycopodium alpinum*), the dark-flowered *Nigritella nigra*, and several other sub-alpine orchids; a number of small, sometimes tiny, gentians (*Gentiana nivalis*, *G. prostrata*, *G. glacialis*, *G. nana*, *Lomatogonium Carinthiacum*), *Valeriana celtica*, the Scottish asphodel (*Tofieldia borealis*) of the north, a few grasses, sedges, and rushes (e.g. *Agrostis*

*alpina*, *Carex curvula*, *Juncus trifidus*), various anemones, campions, umbelliferous plants, violets and campanulas (e.g. *Anemone alpina*, *Silene Pumilio*, *Meum Mutellina*, *Viola alpina*, *Campanula alpina*) and several mosses (e.g. *Dicranum elongatum* and *Polytrichum strictum*) which clothe the humus on stretches of turf and in inclosures.

Many of the plants also that are native on the black graphitic soil in hollows of high mountain ridges take up organic food from their substratum. These include *Meesia alpina* and various other mosses produced exclusively in places of the kind; and, above all, numerous Primulaceæ and Gentianæs (*Primula glutinosa*, *Soldanella pusilla*, *Gentiana Bavarica*). It seems, moreover, to be by no means a matter of indifference to these plants at what temperature, and in what state of the air, in respect of moisture, the decomposition of humus takes place. If species which grow abundantly in these localities are dug up and transferred, together with the black earth in which their roots are imbedded, into a garden, and are there cultivated in such a way that the external conditions are as nearly as possible those of the original habitat; or if young plants are reared from seed in the same black humus-filled earth, they thrive only for a short time, soon begin to fade, and within the space of a year are dead; whereas, alpine plants belonging to the same altitude above the sea, but rooted in loamy or sandy earth, flourish excellently in gardens as well. Various moor-plants (e.g. *Lycopodium inundatum*, *Eriophorum vaginatum*, *Trientalis Europeæ*) only live a short time in a garden even though the clods of peat, in which their roots are imbedded, are transplanted with them. This fact can scarcely be explained except by supposing that the organic compounds, produced by the decay of vegetable remains on alpine heights and moors, are essentially different from those evolved by similar matter under the changed conditions of temperature and moisture occurring in a garden at a lower level. Gardeners say that the peat and black graphitic soil from the slopes of snowy mountains turn sour in gardens, and they may be to this extent right, that in all probability the humic acids produced under altered circumstances are different.

#### SPECIAL RELATIONS OF SAPROPHYTES TO THEIR NUTRIENT SUBSTRATUM.

In the plants under discussion, the cells which absorb organic compounds are, taken all in all, very similar to those which absorb mineral food-salts. Where there is no cell-membrane, as in the case of Plasmodia and Euglenæ, the food diffuses through the so-called ectoplasm, or outer layer of the protoplasm, into the interior of the cell. Saprophytic marine and fresh-water algae are able to absorb the products of decay in the water around by means of their superficial layers of cells. The mycelia of fungi have the power of taking in nourishment with special rapidity. Each hypha, or more accurately, each long, delicate-walled cell of a mycelium is, to a certain extent, an absorptive cell; its entire surface is capable of exercising the function of suction and of withdrawing from the environment, along with water, the very substances which are needed. The coral-like underground stem of

*Epipogium aphyllum*, as well as that of the "Coral-root", which is entirely destitute of roots, develop fascicles of absorptive cells on their ramifications, and on special little swellings; and the white subterranean stem structures of *Bartsia alpina* are also provided with long absorptive cells. The white, fusiform, tuberously thickened, underground stems of the Alpine Enchanter's Nightshade (*Ciræa alpina*) exhibit no roots during autumn and winter, nor until such time as new leafy stems sprout from them and lift themselves into the daylight; they only have scattered club-shaped absorptive cells. Yet it is inconceivable that the few absorptive cells meet the entire requirements of these plants at the season of the development of stems above ground. Food is absorbed in these cases also by the epidermal cells of the entire tuber, underground stem, or coral-like rhizome, as the case may be. The epidermal cells of these subterranean caulomes which lie immediately in contact with the black mould or humus on the ground of forests, have such thin and tender walls that they are quite as well adapted to the absorption of nutriment as are the projecting absorptive cells; indeed the club-shaped absorptive cells on the small tubers of Enchanter's Nightshade exhibit somewhat thicker walls than those forming the general epidermis of the tubers.

We may compare food-absorption as performed by these coral-like and tuberous structures, imbedded in decaying plant residues, with the action of tape-worms in process of sucking in through their entire epidermis the fluid filling the intestines they inhabit. The epidermal cells of the thick tortuous root-fibres of *Neottia Nidus-avis* are all capable of absorbing nutriment, though they do not project as tubes, but are tabular, and have their outer walls, which are in immediate contact with the nutrient soil, only slightly arched outwards (see fig. 16<sup>2</sup>). The green leafy orchids rooted in the vegetable mould of woods and meadows are, on the contrary, furnished with very long tubular absorption cells; and these cells do not wither and collapse forthwith when the root elongates, but long retain their vigour and activity. Whereas in the case of land plants adapted to mineral food-salts, the tubular absorption cells ("root-hairs") are limited to a narrow zone behind the growing point of the root and always die comparatively soon; in the case of orchids, having cylindrical roots imbedded in vegetable mould, these structures appear to be beset from end to end with long scattered tubular absorption cells, which are retained even through the drought of summer or the frost of winter right into the next period of vegetative activity; and these cells occur most abundantly in parts of the ground where there happens to be a bed of humus or mouldering remains particularly amenable to their purpose. Similar relations are found to exist in the case of the dichotomously-branched roots of the Club-moss. They are twisted in spirals and bore into the vegetable mould like corkscrews, and their absorption cells form in some places regular tassels, which are completely cemented over with fine black mould. The roots of grasses which, like the Mat-grass, live on the decomposition-products of vegetable mould, are also distinguished by strikingly long absorption cells, which grow in black or brown humus and there undergo the strangest bends and contortions. When, for instance, a fragment of a dead root or

underground stem, peculiarly desirable for absorption, is encountered, it is regularly embraced by the suction cells, and as great an absorbent surface as possible is thus brought into contact with the nutritious fragment. Indeed, the development of suction cells on the roots of many gentians (viz. *Gentiana ciliata*, *G. germanica*, *G. Austriaca*, and *G. Rhætica*) is confined to the parts of the root-branches, which, in the course of their passage through the vegetable mould, have come into contact with a particularly nutritious portion of it. Wherever there is contact, the root is thickened, and absorption cells project unilaterally from the epidermis and grow into the decaying fragment of wood or bark which is to be drained of its nutrient

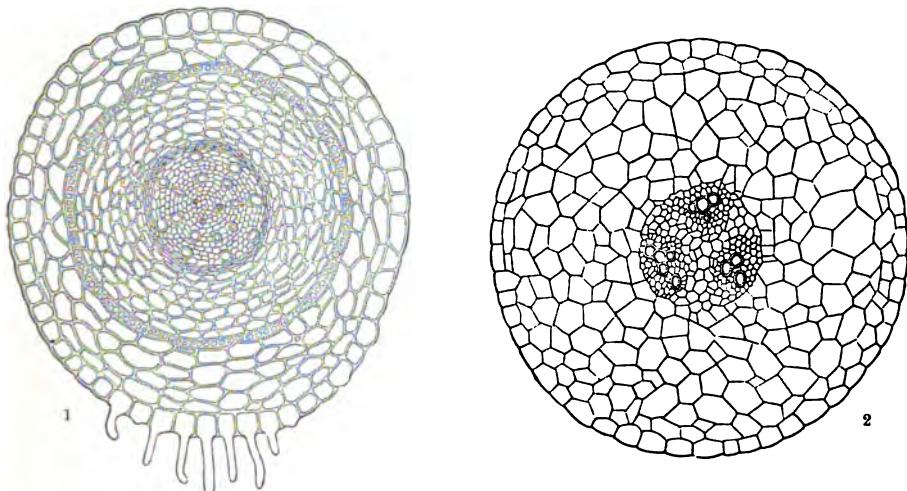


Fig. 16.—Transverse section through absorption-roots of Saprophytes.

<sup>1</sup> *Gentiana Rhætica*.

<sup>2</sup> The Bird's Nest Orchis (*Neottia Nidus-avis*).

material (see fig. 16<sup>1</sup>). Roots of this kind remind one of the root-structures of parasites which are furnished with so-called "haustoria", and which will be discussed more in detail in subsequent pages. But they are different in that they absorb food not from living but from decaying parts of the nutrient substratum.

Most plants that grow on the vegetable mould of alpine meadows, and the black earth deposited by snow-drifts in mountainous regions, develop flat instead of tubular epidermal cells as suction cells, and in this resemble marsh-plants. In many of these cases the roots are so abundantly and minutely ramified that they form a plexus investing the humus. This is likewise true of the absorptive cells on the rhizoids of mosses.

Plants which lie flat against the bark of trees and have no connection with the ground, so that they are unable to derive nutriment from it, have a very peculiar method of maintaining themselves. Their roots, rhizoids, or hyphæ, as the case may be, either grow straight into the bark or are merely adnate to its surface. In the latter case they are exposed on one side to the open air, and form more or less projecting lines and ridges ramifying in all directions, often constituting a regular trellis-work cemented to the bark. Sometimes, too, they are represented

by thicker ropes or bands which run longitudinally down or encircle the trunk. These structures certainly serve as instruments of attachment, but at the same time they also absorb nutriment from the substratum, the decaying bark upon which the plant is epiphytic. In periods of drought the absorption of food by plants of this kind is, in general, interrupted and suspended. But when the rainy season commences and there is a long duration of wet weather, water trickling over the surface of boughs and trunks washes the bark, cleanses it as it were, and, falling lower and lower, brings down not only tiny loosened particles of bark but mineral and organic dust which has been blown into it by the wind; it dissolves all the soluble matter it finds on its way, and so reaches the roots, rhizoids, and hyphæ which adhere to the bark, in the form of a solution of mineral and organic compounds, chiefly the latter. The trickling water is in some measure stopped by the projecting ridges of these adnate structures; here and there also it deposits particles mechanically suspended in it, and so it conveys to these curious epiphytes the requisite nourishment.

In the same way, no doubt, epiphytes which grow upon other epiphytes are nourished. In more inclement regions, the green bark, stem, and, less frequently, the green leaves of the mistletoe are found to be beset by mosses and lichens; and, in the tropics it is a common phenomenon for mosses, liverworts, and even small kinds of Bromeliaceæ to settle on the green and still living leaves of Bromeliaceæ, Orchideæ, and Loranthaceæ, although they are certainly not properly parasitic, and only use their absorption cells for the purpose of clinging to the thick epidermis of the living leaves or stem which support them. The principal part of the liquid substances absorbed by these plants is conveyed to them by the rain-water that washes over the substratum.

The species of plants also which have been mentioned as sometimes growing on smooth vertical faces of rock, though the bark of trees is their usual habitat, are able to obtain their food-materials in a similar way. If the summit of a cliff is covered by a continuous carpet of plants, or if ledges and terraces projecting somewhat from its face support sods of grass, tufts of moss, and various small kinds of bushes, it must inevitably happen when there is an abundant fall of rain that the water flowing down the declivity conveys with it organic compounds in solution. First the sods of grass and moss on the ledges and on the top of the cliff are wetted, then the humus, which is their substratum, becomes saturated, and such part of the water as cannot be retained by this humus, or does not percolate into the cracks and crevices of the rock, trickles down from the ledges and moistens the face of the rock as it soaks down to the bottom. A rocky declivity is thus washed in the same way as is the bark of trees, and small fragments of organic and inorganic bodies must of necessity be rinsed out and carried down by the trickling water, and then again be deposited in heaps where projecting obstacles are encountered. It is just in the tracks along which the water flows down steep rocks of the kind that the plants of which we have made mention are situated.

Associated with the above are generally a number of other plants, for the most

part microscopic, all of which cannot be classed as saprophytes, but which, in order to be able to thrive in the tracks of trickling water, must have the capacity of surviving desiccation for weeks, and even months, on the barren rock after having been previously supplied with copious moisture for a time. In the case of lichen-growths in particular these are very favourite sites; and when the lichens cover a large area they attract one's attention from afar. In limestone ranges, the light-gray rock of steep declivities, interrupted by ledges covered with grass and low brushwood, is extensively coloured by dark vertical bands and streaks, and the effect is the same as if a dye had flowed from the ledges over the face of the rock. These dark streaks indicate the course of the water which oozes from the humus and renders possible the existence of numberless minute plants on the precipitous face, in particular several dark crustaceous lichens (*Acarospora glaucoarpa*, *Aspicilia flava*, *Lecidea fuscorubens*, *Opegrapha lithyrga*, &c.).

The quantity of organic compounds brought down in solution by the water which filters from the layers of humus on rocky ledges, and that which trickles down the bark of trees, is, however, very small. Still, it is amply sufficient to meet the requirements of the plants occurring at the spots in question. The claims made by them upon their nutrient source are very moderate. We may here recall the instances previously mentioned of mycelia of fungi which have been found satisfied with the scarcely perceptible quantities of organic compounds in water filtering into the shaft of a mine, and in the pure water of a mountain spring respectively. To these instances must here be added the production of mycelia in the wooden pipes through which the clear water of mountain springs is conveyed. After these pipes, which are made from the trunks of pines, have been used as conduits for years, and their inner layers of wood have long since been washed out, the mycelium of the fungus *Lenzites sepiaria* is not infrequently developed within them, and in such luxuriance, indeed, that it forms great yellowish-gray flocculent masses, which issue from the pipe's inner surface, and float in the stream of running water. In time these flocculent masses increase in the clear spring-water to such a degree that the pipes become completely blocked, and the flow of water is arrested. And yet the water conducted through the pipes is so pure, where it enters into and issues from them, that the residue obtained by the evaporation of hundreds of litres afforded no trace of any organic matter.

Seeing that most saprophytes absorb only such a comparatively small amount of organic matter, one is all the more surprised to notice that a large number of them fall suddenly, at certain times, into the opposite extreme. People speak of things rapidly produced in abundance as "mushroom-growths", and as "shooting up like fungi". The fructifications of many fungi are in fact developed with a rapidity which borders on the miraculous. The various species of *Coprinus* living on dung produce their long-stalked, cap-shaped fructifications during the night, and by the evening of the next day the caps have already fallen to pieces, and are in a state of decomposition, and nothing is to be seen in their place but a black deliquescent mass like a blot of ink. The weight of this fructification, thus matured within

twenty-four hours, is certainly many times as great as that of the entire mycelium which produced it; and it is quite incomprehensible how this mycelium, which for weeks only achieves a moderate development, and adds but little to its dimensions, is in a position suddenly, and in so short a time, to supply the amount of water and organic compounds requisite for the building up of the fructification. *Epipogium aphyllum* exhibits a similar property. After producing nothing for two years excepting a few branches on its subterranean stem, it develops all at once and in a very short space of time fleshy stems with large flowers, and one asks with astonishment how the relatively small coral-shaped stock sets about obtaining the quantity of nutrient materials necessary for the construction of these flowering stems. We are here confronted again with the great mystery of periodicity, the solution of which we must for the present forego.

Saprophytes are much more fastidious as regards the quality of their nutriment than one might expect. It is true that certain fungi are produced wherever there are plants in a state of decomposition, and to them it is quite indifferent whether the mouldered dust, which serves as a nutrient soil for their mycelia, has arisen from one species or another. Also in the case of orchids imbedded in vegetable mould, and in that of most of the mosses and liverworts adherent to the barks of trees, it is, as a rule, of no consequence whether the tree constituting the substratum is a conifer or a dicotyledon. But a large number of species are associated with the decaying remains of particular plants or animals only. For example, certain small species of *Marasmius*, belonging to the group of the Agarici, occur only on mouldering pine-needles; another small fungus, *Antennatula pinophila*, is found exclusively on fallen needles of the Silver Fir; *Hypoderma Lauri*, which resembles small black type on rotting laurel leaves, and the tiny *Septoria Menyanthis* on leaves of the Bog-bean (*Menyanthes trifoliata*) lying under water in a state of decay. The cinnamon-coloured receptacles of *Lenzites sepiaria* only grow from prostrate trunks of conifers, and the black fuliginous fructifications of *Bulgaria polymorpha* only on those of oaks. A small discoid fungus named *Poronia punctata*, white with black spots on the top, is only found on cow-dung; another fungus, *Gymnoascus uncinatus* on that of mice, and *Ctenomyces serratus* on decaying goose feathers.

That many mosses are also very fastidious in the selection of their substratum has already been intimated. Just as in the Alps *Splachnum ampullaceum* is only found growing on the putrefying dung of cattle, so in arctic regions the splendid, large-fruited *Splachnum luteum* and *S. rubrum* occur exclusively on that of reindeer. *Tetraplodon urceolatus* is met with on mountains always with decaying excrements of chamois, goats, or sheep for a substratum, whilst *Tetraplodon angustatus* chooses the excrements of carnivorous animals, and *Tayloria serrata* is only seen near cow-chalets on decomposing human faeces. The circumstances of the occurrence of another moss belonging to the Splachnaceæ, i.e. *Tayloria Rudolfiana* is also very interesting. It grows usually on the branches of old trees, especially maples in sub-alpine regions, and one is tempted to believe that in respect of its nutrient substratum it is an exception to the rule of the rest of the

*Splachnaceæ*. But on closer examination there is convincing evidence that this moss also only lives on animal dung undergoing putrefaction. For remains of broken mouse and bird bones are invariably to be discovered in the substratum, and there can be no doubt that the *Tayloria* chooses for its site boughs of old trees upon which birds of prey have dropped their excrements. Of the mosses living on the bark itself, one instance is also worth mentioning. Whereas in the case of most species of the genus *Dicranum*, the mouldering residues of conifers constitute the favourite substratum; there is one species, viz. *Dicranum Sauteri*, which is found only on the bark of the beech. The weather-worn bark of this tree is seen, in sub-alpine districts, covered with the most brilliant emerald-green films of the above-named moss; whilst on adjacent pines and fir-trees no trace of it can be found.

#### PLANTS WITH TRAPS AND PITFALLS TO ENSNARE ANIMALS.

A number of plants exhibit contrivances which obviously have for their object the capture and retention of such small creatures as may fly or creep on to their leaves; and it has been ascertained by searching experiments that the majority of these plants use the animals they capture, in one way or another, as sources of nutriment. For the most part the animals that are caught are insects, and hence the term "insectivorous plants" has been applied to the class in question. The flesh of the insect being the part of it principally serviceable for food, the name "carnivorous" or "flesh-eating", or better, perhaps, "flesh-consuming" plants has also been used; and seeing that the most important part of the whole process is really the digestion, or taking in of organic compounds from the captured animals after they are dead, we might call those plants which are furnished with organs for the absorption of the dissolved flesh of animals ensnared by them, "flesh-digesting" plants as well. As will appear from the following discussion of the subject, no one of these names completely covers the wonderful phenomena in question, and it is scarcely possible to find a short and not too cumbrous expression which shall henceforward exclude all misconceptions.

In round numbers we may estimate the plants which capture animals and demolish them for food at five hundred. Within this comparatively small range, however, the variety of the mechanism for seizure and absorption of nutritive matter is so great that in order to give a general picture of them it is necessary to classify them into several sections and groups. In the first section we have a series of plant-forms wherein chambers are developed, which admit of the entrance of small animals, but not of their escape. The organs of capture and digestion of the plants belonging to this section exhibit no external movements of any kind, and are thereby differentiated from the forms belonging to the second section, which perform definite movements, in response to a stimulus caused by the contact of the animals, with the object of covering the prey with as great a quantity of digestive fluid as possible. Lastly, there is a third section wherein the individual forms are

neither provided with pitfalls nor capable of performing special movements, but have leaves converted into lime-twigs and on them animals stick and are also digested.

The first and most extensive group included in the first section is that of Utriculariæ or Bladderworts. Their capturing apparatus consists of little bladders with orifices closed in each case by a valve, which permits objects to penetrate into

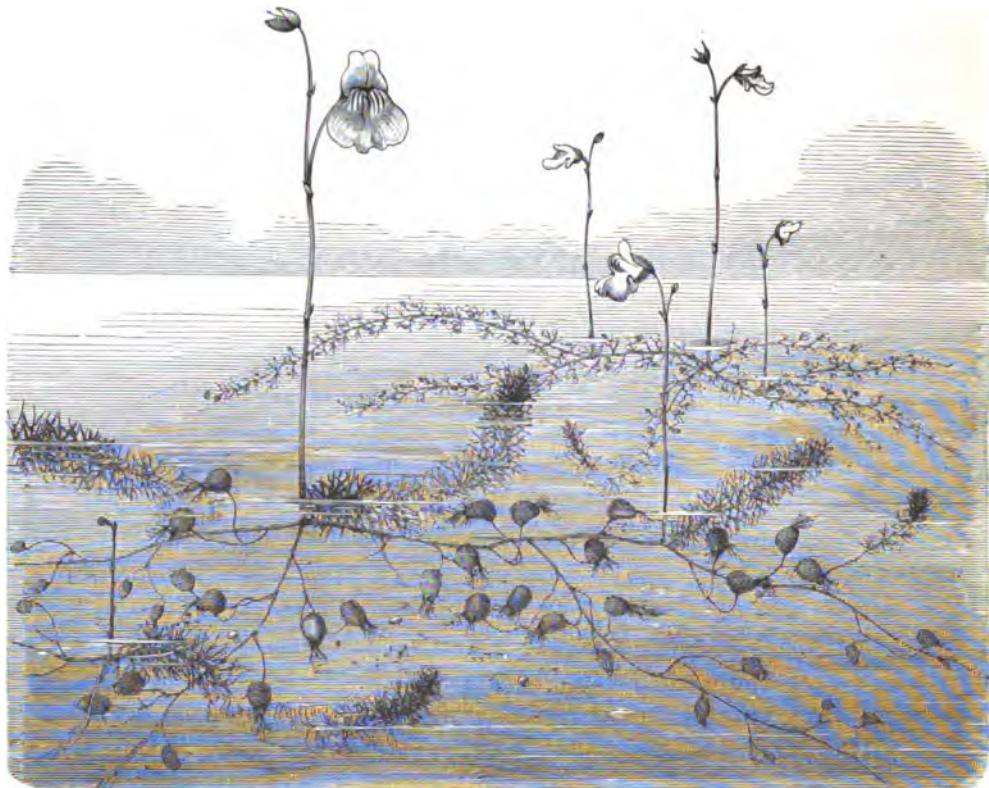


Fig. 17.—Bladderworts.

In the foreground *Utricularia Graftana*; in the background *Utricularia minor*.

the cavity of the bladder, but not to issue out of it. The Utriculariæ are rootless plants which live suspended in water, and, according to the season of the year, either sink down to the bottom or ascend to just below the surface. Upon the approach of winter, when animal life is gradually disappearing in the chilled and freezing upper layers of water, the leaves at the extremities of the floating stems are enlarged and form spherical winter buds; the older parts of the stems together with the leaves die, their cavities hitherto occupied by air are filled with water, and they sink to the bottom drawing down with them the winter buds. After the winter these buds elongate, detach themselves from the old stems and ascend near the surface, where innumerable little aquatic animals are swimming to and fro, and there develop two rows of lateral branches in rapid succession. Either all of these are thickly covered with leaves which are divided into thread-like, repeatedly

bifurcating, segments, or else only half of them are thus clothed with leaves whilst the other half bear the before-mentioned bladders. The former is the case in *Utricularia minor*, the plant represented in the background of the figure on p. 120; and the latter in *Utricularia Grafiana*, which is drawn in the foreground. In instances of the former kind obliquely ellipsoidal bladders are to be seen on short stalks on the principal segments of the leaves, usually quite near their angles of bifurcation. In the smaller species, such as *Utricularia minor*, they have a diameter of about 2 mm. In individuals of the latter kind the bladders have longer stalks, and are about 5 mm. in diameter. They are always pale-green and partially transparent. Each bladder is somewhat flattened at the sides and exhibits a markedly convex dorsal surface and slightly curved lateral surface. An orifice, whose border is fringed with peculiar stiff tapering bristles, leads into the interior of each of these stalked bladders. The aperture has four rounded angles and is framed as it were, by a pair of lips. The under lip is strongly thickened, and is furnished with a solid cushion projecting into the interior of the bladder.

From the upper lip hangs a thin transparent, obliquely-placed valve (see fig. 18<sup>2</sup>), the free edge of which rests upon the inner surface of the cushion before referred to, and closes the entire orifice. This valve is very elastic and yields easily to any pressure from outside. A tiny animal is able, by pressing against it, to force a way without difficulty from the nether lip into the interior of the bladder, and to slip in through the opening thus made. But as soon as the animal has got inside, and ceases to press upon the valve, its elasticity brings it back upon the under lip again. It cannot be opened by pressure from within; for, resting as it does upon the projecting cushion, it is impossible for the little prisoner to force it over the latter in an outward direction.

The whole apparatus forms a trap for small aquatic animals, they being able, as before observed, to slip into the bladder but not to get out again. Most animals that enter make, it is true, efforts to escape, but they are all in vain. Many perish in a short time—about twenty-four hours—others live from two to three, or, in some cases, even as much as six days. But in the end they must suffer death by suffocation or starvation, and they then decay, and the products of their decomposition are sucked in by special absorption cells developed within the bladder. These absorption cells (see fig. 18<sup>3</sup>) are linear-oblong and somewhat like little rods in shape, and they line the whole internal surface of the cavity of the bladder. They are arranged in fours, each group of four forming a cross and being united by a

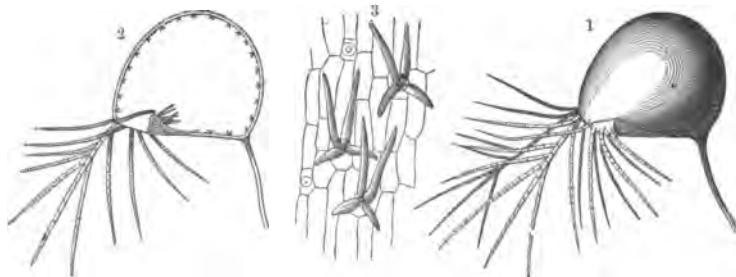


Fig. 18.—Traps of *Utricularia neglecta*.

<sup>1</sup> A bladder magnified ( $\times 4$ ). <sup>2</sup> Section of a bladder. <sup>3</sup> Absorption-cells on the internal surface of the bladder ( $\times 250$ ).

common basal cell. The basal cells themselves are intercalated amongst the cells lining the bladder. The organic substances from the decaying bodies of captured animals are sucked up by these stellate groups of cells, and from them pass into the basal cells, and later, into the other adjacent cells of the bladder and those of the plant at large.

The majority of the animals caught by the bladders are crustaceans. It is principally larvæ and adult individuals of small species of *Cypris*, *Daphnia*, and *Cyclops* that fall into the trap; but larvæ of gnats, and various other small insects, little worms, and infusoria, are also not infrequently met with imprisoned in the bladders. The number of animals captured is comparatively large. In single bladders the remnants of no less than twenty-four small crustaceans have been observed. The prey secured by *Utricularia minor* (fig. 17), which lives in little pools of still water in peat-bogs, is very abundant. The North American *Utricularia clandestina* seems also to use its capturing apparatus with great success.

What it is that induces the animals to press upon the valves and so fall into the trap is not fully explained. We may suppose that they expect to find food in the bladder-cavity, or that they hope it will afford a shelter where they can rest for a time and be protected from their pursuers. The last suggestion is especially supported by the circumstance that the approach to the valve-covered orifice of the bladder is guarded against the intrusion of larger animals by stiff sharp bristles which stick out from it (fig. 18<sup>1</sup>). Only very small animals, which can easily slip in between the relatively large bristles, reach the inside of the bladder, whilst larger creatures, which would injure the whole apparatus, are prevented from coming near it. Thus, the most probable explanation is that lesser animals pursued by greater take refuge in the hiding-places behind the bristles, and so fall into the trap. Another very striking fact is that the bladders of Utriculariæ, living in still water, look delusively like certain Ostracoda, especially species of the genus *Daphnia*. The bladder itself resembles the shell-covered body in size and form, and the bristles the antennæ and swimmerets of one of these crustaceans. Whether there is any significance in this curious similarity of outward appearance must be left undecided.

The majority of Utriculariæ live in pools of water beside foot-tracks on moors and in the little collections of water between clumps of reeds in peat-bogs; and these are precisely the haunts of the little creatures that are to fall into the traps. Every handful of water that one scoops up contains hundreds of midge-larvæ, water-fleas, Ostracoda, and one-eyed Cyclops, which rush about promiscuously, pursuing and seizing one another. One species of these plants lives in the mountains of Brazil in the rain-filled receptacles of *Tillandsia* plants. The *Tillandsia* is allied to the pine-apple, and has rosettes of concave leaves, the latter resting one upon the other in such a way as to form a niche or cavity in front of each leaf which fills with rain like a cistern. Many different kinds of small animals are always swimming about in these little cisterns, and almost every one of the latter

is the sphere of activity of an individual *Utricularia nelumbifolia*. This plant is remarkable also from the fact that long runners are thrown out from its stems, which grow across, in wide arches, from its cistern to a neighbouring *Tillandsia*, where it selects one of the reservoirs in the rosettes as a new site and dips down into the water—a fantastic method of propagation of which we shall speak again on another occasion.

A few *Utriculariae* do not live in water at all, but grow amongst mosses, liver-worts, and lycopods, in the vegetable mould filling the clefts and crevices of rocks, and the bark-fissures of old trees. Of this habit, for example, is the pretty Brazilian *Utricularia montana*, which, in spite of the difference of its habitat, is provided with an apparatus for capturing animals agreeing in all essential respects with the description already given. The bladders used by these plants for purposes of prey are produced on subterranean filiform stems which thread their way in the vegetable mould and wefts of decaying moss-stems, and here and there swell into tubers. The bladders are hyaline and transparent, and are filled with watery liquid, sometimes also with air. They are only 1 millimeter in diameter, but are present in large numbers. The entrance into these bladders is much more concealed than in the species that live in water. The dorsal surface of the bladder being still more highly curved, the position of the orifice is altered so as to be quite close to the little stalk of the bladder. In addition, the orifice is, as it were, roofed over, and thereby protected against the possibility of being stopped up by particles of earth, and the passage leading to it is very narrow. That, in spite of the difficulty of entrance, a number of minute animals do seek a hiding-place here is proved by the circumstance that, besides various infusoria, rhizopoda, and creatures of that kind inhabiting damp earth, species of *Acarus* and larvæ of other animals have been found, both dead and alive, in the bladders.

With this first group of insectivorous plants, wherein the capturing apparatus includes a valve to prevent the egress of such animals as fall into the trap, is associated in the first section a second group, viz. that of the ascidia-bearing or pitcher-plants, in which the foliage-leaves are converted into pitfalls, and the escape of the captured prey prevented by a number of points lining the inner wall of the cavity, and directed from the aperture towards the closed bottom. There is an extraordinary variety in the form of the pitfalls. Sometimes they are tubular, utricular, or funnel-shaped cavities, sometimes mug or pitcher-shaped, or urceolate; in some cases these are straight, in others bowed like sickles, or spirally twisted. They always arise from the part of the petiole upon which the lamina immediately rests. The lamina is always relatively small, being represented in the majority of the traps by a scale or lobe, and it only appears to be an appendage of the large expanded and hollowed-out petiole. In many pitcher-plants the little lamina looks like a lid placed over the orifice to the pitfall, as, for instance, is shown in the illustration (fig. 21<sup>4</sup>), whilst in others (*Nepenthes ampullaria* and *N. vittata*) it has the form of a handle or stalk, and serves as a place for animals visiting the pitchers to alight upon.

In each pitfall there are always three kinds of contrivance to be distinguished: first, a device for the allurement of animals; secondly, an arrangement for entrapping the prey enticed, which at the same time prevents individuals once imprisoned from returning and escaping through the entrance hole; and thirdly, a structure for causing the decay or dissolution of the dead animals at the bottom of the pitfalls, and for rendering possible the absorption of the products of decomposition as nutriment. The means of allurement are similar to those which cause the visits of small creatures to flowers, that is to say, principally honey and bright and varied coloration, whereby the nectar-secreting spots are recognized from afar, especially by flying insects. The escape of animals when they have once entered the cavity of a petiole is prevented, as has been already mentioned, by a fringe of sharp hairs pointed downwards, or by various spinous structures on the inner

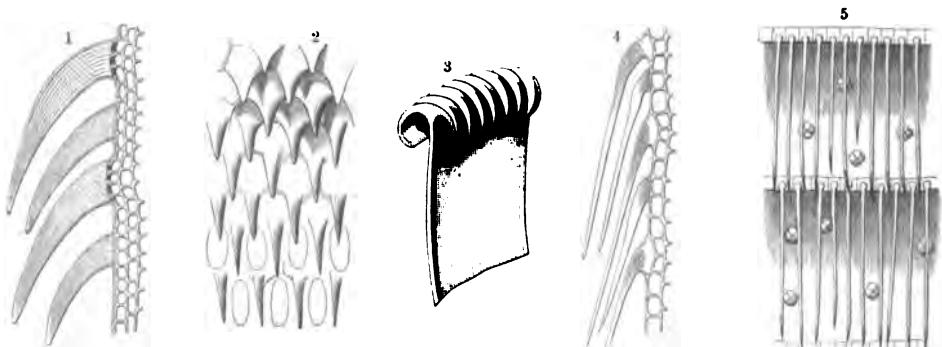


Fig. 19.—Spinous Structures in the Pitfalls of Carnivorous Plants.

<sup>1</sup> *Genlisea*; a piece of the tube seen from inside. <sup>2</sup> *Heliamphora nutans*; spines on the walls of pitfalls. <sup>3</sup> *Sarracenia purpurea*; a piece of the lining of the pitcher near the orifice seen from inside. <sup>4</sup> *Sarracenia purpurea*; longitudinal section through the membrane covered with spinous bristles in the lower part of the pitcher. <sup>5</sup> *Nepenthes hybrida*; fringe of spines at the orifice of the pitcher. <sup>1, 2, 4, 5</sup> greatly magnified; <sup>3</sup> slightly magnified.

surface of the cavity. The decomposition and dissolution of the prey are effected by fluids secreted by special cells at the bottom of the utricles and pitchers.

But although in respect of the consecutive and co-ordinate operation of these three kinds of contrivance, all ascidia-bearing and pitcher-plants resemble one another, there are considerable individual divergences as to structure and function that it is well worth while to study in some detail the most noticeable of them.

One of the most noteworthy is the genus *Genlisea*, which is nearly related to Utriculariaceæ in the structure of its flowers and fruit. It is composed of a dozen species growing in water and marshy places. Of these one is a native of tropical and southern Africa, whilst others are found in Brazil and the West Indies. In addition to ordinary leaves, which in them are spatulate, most of the *Genliseæ* possess leaf-structures metamorphosed so as to constitute pitfalls. Each pitfall consists of a long, narrow, cylindrical utricle, which at its blind end is enlarged into a bladder, whilst the narrow orifice at the opposite end are placed two peculiar ribbon-shaped processes twisted spirally. The orifice of the utricle is set with very small sharp teeth bent inwards; and the tubular part of the utricle has its inner surface lined throughout with innumerable little bristles, which arise from rows

of cells forming inwardly projecting ridges, and have their sharply-pointed tips directed downwards (see fig. 19<sup>1</sup>). Amongst these needles are also found, scattered over the whole internal surface, roundish wart-like glands or papillæ, composed of four or eight cells. The bottom of the bladder-like cavity in which the utricle terminates is destitute of bristles, but provided only with glands arranged in rows. Small worms, mites, and other segmented animals which enter through the orifice of the utricle can easily reach the enlarged base. But as soon as they try to com-

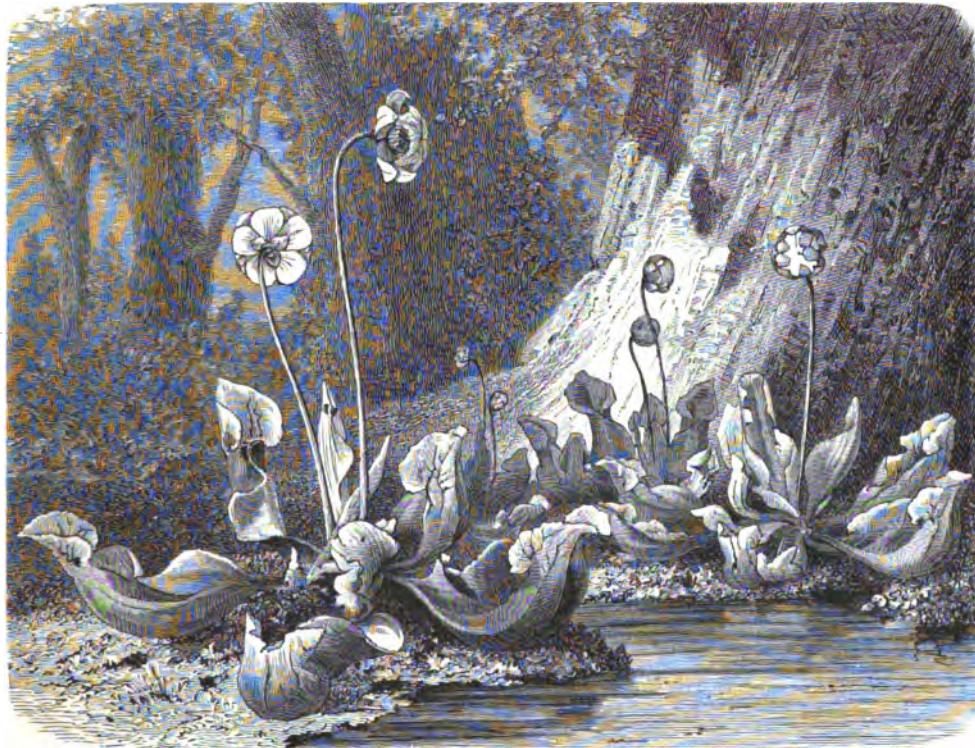


Fig. 20.—*Sarracenia purpurea*.

mence the return journey they are opposed by the points of a thousand bristles. Thus caught they die, and the products arising from the decay of their bodies are absorbed by the glands situated, as above mentioned, at the bottom of the bladder and on the walls of the utricle.

As types of a second series of carnivorous plants belonging to the group of pitcher-plants may be taken *Heliamphora nutans*, a native of moorlands on the mountains of Roraima, on the borders of British Guiana, and *Sarracenia purpurea* (see fig. 20), which is widely distributed in the marshes of eastern North America from Hudson's Bay to Florida. In both instances the leaves metamorphosed into ascidia are arranged in rosettes, rest their bases on damp earth and thence curve upwards. They are somewhat inflated, like bladders, at about their middle, but contract again at the orifice where they pass into the relatively small laminæ. The latter are threaded by red streaks like blood-vessels, have the form of valves,

and turn their concave surfaces towards falling rain. They serve, moreover, at least in *Sarracenia purpurea*, to catch the drops of rain, which then flow down into the bottom of the ascidia and fill them more or less with water. There is very little evaporation from the hollow pitchers; and even when there has been no rain for a week, one always finds some of the previously-collected water at the bottom. The inner surface of a pitcher is lined by cells arranged like the scales of enamel on a pike's back (see fig. 19<sup>2</sup>). The internally-projecting wall of each of these scales is transformed into a stiff decurved point, and the lower the position of the cells the longer do the points become. The shell-like lamina again, above the contracted orifice, bears glandular hairs which exude honey, so that the parts surrounding the aperture are covered by a thin film of sweet juice.

Many animals are attracted by this honey. Some are winged and alight from flying; others, being wingless, make use of a peculiar ridge, which projects on the concave side of the utricle, to help them to creep up the latter. If these honey-eaters happen to travel away from the lamina to that part of the pitcher which is lined with the smooth and slippery decurved cells, they are as good as lost. They slip down over the brink, every attempt to climb up again being rendered futile by the downwardly-pointing needles which clothe the lower part of the wall; and ultimately they fall into the water collected at the bottom, where they are drowned and their bodies putrefy. The products of decay are absorbed as nutriment by the epidermal cells in this region. The number of animals meeting with this fate is often so great that an offensive odour, arising from the decaying bodies, is emitted by the utricles and is noticeable at a considerable distance. In the wild state, the ascidiform utricles are often half-full of drowned animals and it is stated that in these circumstances birds also put in an appearance and pick some of the dead remains out of the utricles.

Whether the liquid filling the bottom of the pitchers consists simply of rain-water, or whether the latter is modified by a secretion originating in the gland-like groups of cells there (see fig. 28<sup>7</sup>), is still uncertain. A centipede over 4 centimeters long having fallen into a utricle of *Sarracenia purpurea* in the night was found only half immersed in the water. The upper half of the creature projected above the liquid, and made violent efforts to escape; but the lower part had, after a few hours, not only become motionless but had turned white from the effect of the surrounding liquid; it appeared to be macerated, and exhibited alterations which are not produced in so short a time in centipedes immersed in ordinary rain-water. When a number of captured animals are undergoing putrefaction at the same time in a pitfall, the liquid turns brown and has the appearance of manure-liquor.

There is a great difference between the utricles of *Sarracenia purpurea* and the apparatus adapted to the capture of prey in the plants of which we have chosen as examples, *Sarracenia variolaris*, a native of the marshes of Alabama, Florida, and Carolina, and the *Darlingtonia Californica*, found growing at a height of from 300 to 1000 meters above the sea on moorlands in California from the borders of

Oregon to Mount Shasta. In both of these the liquid with an acid reaction, which fills the bottom of each utricle, is certainly only secreted by the cells in the interior of the cavity itself, and it is quite impossible that a single drop of the rain or dew deposited upon the plant should reach the interior of the cavity. The hollow petiole is in both plants, above mentioned, utricular or tubular, and only slightly

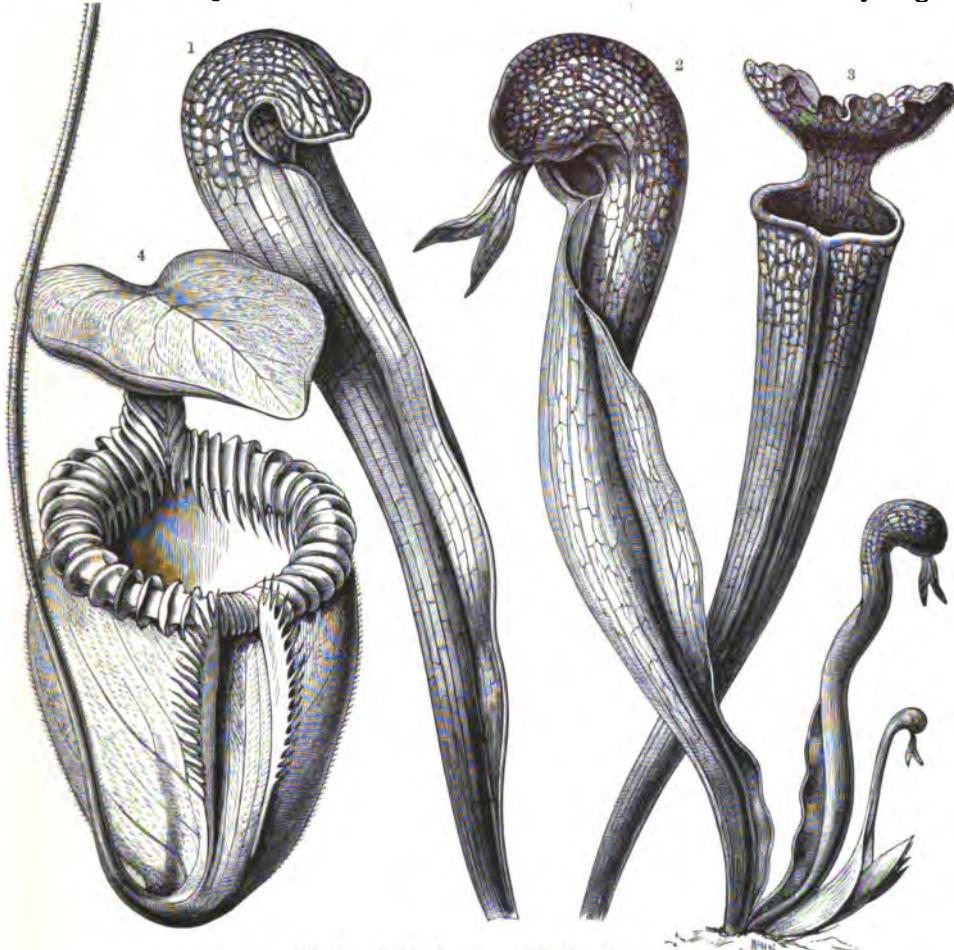


Fig. 21.—Ascidia-bearing and Pitcher-plants.

<sup>1</sup> *Sarracenia variolaris*. <sup>2</sup> *Darlingtonia Californica*. <sup>3</sup> *Sarracenia laciniata*. <sup>4</sup> *Nepenthes villosa*, reduced to one-half natural size.

enlarged towards the top. The dorsal side of each leaf is, however, at its upper end hollowed out like a cowl or a helmet, and forms a cupola as is shown in fig. 21<sup>1</sup> and 21<sup>2</sup>. The orifice or entrance into the utricle is consequently covered over and is reduced to a slit or hole under the hood. The lamina is transformed into a lobe, which in *Sarracenia variolaris* is small and roofs over the orifice of the utricle, and in *Darlingtonia* is shaped like the tail of a fish, and hangs down in front of the aperture. The lower part of the utricle is of a uniform green colour, but the upper part (*i.e.* the cupola and lobe-like appendage) has red ribs and veins, and here and there is quite purple. Between the veins the

leaf is thin, translucent, and pale-green or whitish; and these clear translucent patches, framed by purple or green ribs, look as if they were little windows, especially when seen from within the utricle. The mixture of green, red, and white gives the upper parts of the leaves such a gay appearance that, from a distance, they might be mistaken for flowers.

Insects are doubtless attracted by these bright colours, and both round the orifice, and on the inner surface of the cupola, they find exudations of honey which they suck or lick up with avidity. In *Sarracenia variolaris*, honey is to be seen besides, on the edge of a broad free border which is decurrent along the utricle, and extends from the ground to the orifice. This border forms a favourite path for wingless insects, especially ants, which are particularly eager in their quest for honey. For them it is a sure way to destruction, for when they, gradually following the honey-baited pathway, arrive at the orifice to the utricle and pass through it, they inevitably get upon the smooth decurved points of the epidermal cells, constructed just like those in *Sarracenia purpurea*, and then, unable to stop themselves, slip down to the bottom of the pitcher. When small winged insects alight from flying and fall down the slide into the interior, they make use of their wings in the hope of saving themselves, but they never succeed in finding the aperture by which they entered, as it slants downwards and is situated in shadow. They invariably try to escape through the cupola, mistaking the thin portions, through which the light penetrates into the interior, for gaps permitting egress. But just as flies in rooms dash against the windows hoping to pass through them into the open air, so the small insects in the utricles of *Sarracenia variolaris* and *Darlingtonia Californica* knock against these windowed cupolas, in their desire to save themselves by flying through. They always fall down again to the bottom of the utricle as though into a cistern. If they are immersed in the liquid there secreted, or only in partial contact with it, they are stupefied, but not immediately killed. They often live incarcerated for two days, and it would therefore be erroneous to suppose that the fluid in the pitchers acts on the prey as a deadly poison. But it assists the decay and dissolution of the captives as they die of starvation and suffocation, and, as in the case of the utricle-plants previously described, a brown liquor of very unpleasant odour is produced, and there is a residue of solid pieces of skeleton difficult to decompose, such as the wing-cases, claws, and thoraces of various beetles, lice, ants, and other small insects which have shared the same unlucky fate.

The number of animals captured is very considerable. The pitchers of *Sarracenia variolaris*, which attain to a length of 30 cm., are usually found, when growing in their natural habitat, filled to a height of from 8 to 10 cm. with animal remains, and even a heap 15 cm. high has been observed. We must here remark that in the ascidia of *Sarracenia variolaris*, wingless insects, which creep about the earth, are found to predominate, whilst in *Darlingtonia*, on the contrary, most of the insects are winged. The cause of this is easily understood. The former plant has honey exuding on the flap or ridge running down from the orifice to the

ground, and many wingless insects are thus induced to climb up the alluring path and to enter the cavity of the pitcher. *Darlingtonia*, on the other hand, is destitute of honey on its decurrent ridge, and only provides the sweet meal at the top in the vicinity of the orifice, where it is available for flying insects, which, as a rule, only visit nectar-secreting flowers. The purplish-red scale, shaped like a fish's tail, and hung out like the sign-board of an inn in front of the entrance to the pitcher, constitutes an instrument for the attraction, from afar, of these winged creatures, which are endowed with a vivid sense of colour; and, as experience shows, it does not fail in its object.

What significance is to be attributed to the spiral torsion of *Darlingtonia* leaves (see fig. 21<sup>2</sup>) it is difficult to say. Perhaps the escape of animals once imprisoned in the depths of a pitfall is hereby rendered still harder. It would at all events be much more difficult for an insect trying to escape by the use of its wings to ascend a canal which, in addition to being lined with decurved points, was spirally wound, than a canal similar but straight and widened towards the top. We must not omit to mention that a few flies and a small moth have selected as their ordinary habitat the pitchers of both the plants just described, in spite of their being so fatal to most insects. The grubs of a blow-fly (*Sarcophaga Sarraceniae*), in particular, live in large numbers amidst the heaps of decaying insect bodies at the bottom of the pitchers, and are there nourished just as are the grubs of allied species in the rotten flesh of birds and mammals. When mature, the grubs quit the environment of dead remains, passing through holes bored by themselves in the side wall of the pitcher, and turn into chrysalises in the earth. But the fly itself can without danger pass in and out of the pitfalls, which are so perilous in the case of other insects, and it is enabled to do this by means of the special structure of its feet. On the last joint of each foot it has a long claw and sole-like attachment-lobe, and it is able to push these appendages between the sharp, slippery, decurved hairs lining the inner surface of the pitcher, and so to hook itself to the deeper strata of the wall. This apparatus may be likened to the grapple-like climbing irons of Tyrolese mountaineers, and, thus armed, the fly is in a position to ascend the inner wall of a pitcher unscaleable by other insects. The case of the small moth *Xanthoptera semicrocea* is similar. The tibiae of this insect are armed with long, sharp spurs, one pair on each of the two middle legs, and two pairs on each of the two hindmost legs; and, by the help of these spurs it likewise is able to tread uninjured over the dangerous surface of the wall. Its caterpillars, too, cover the sharp slippery hairs with a web, and so render them harmless.

The presence of these animals in the death-traps of *Sarracenia*s is of special interest, inasmuch as it shows that the animals which perish at the bottom of the pitchers are not exactly digested. If maggoty flesh enters the stomach of a carnivorous animal, not only the flesh itself but the maggots as well (which, indeed, immediately die on reaching the stomach) are speedily dissolved by the action of the gastric juice. Such is also the case with several animal-capturing plants to be described in the next pages. But the fluid secreted in the pitchers of *Darlingtonia*

and *Sarracenia variolaris* cannot exercise this digestive action, for if it did the maggots in the heap of rotting insects could not remain alive and well. Its action is limited to the promotion of decay and the formation of a foul liquor, in other words, a liquid manure, which is absorbed as nutriment by the epidermal cells at the bottom of the pitchers.

Another series of pitcher-plants comprises forms in which the petioles are converted into symmetrical sacs with apertures at the top, and the laminae spread out over them like lids for protection. Most frequently the pitfalls in plants of this kind are shaped like pitchers, jars, urns, cups, or funnels; and the lid over the orifice of each cavity is, for the most part, so placed as to prevent rain-drops from falling in, but not to hinder in any way the entrance of animals. In this series are included, firstly, a few species of *Sarracenia*, viz. *Sarracenia Drummondii* and *S. undulata*, next, the Australian *Cephalotus follicularis*, and lastly, the numerous species of the genus *Nepenthes*, which are designated by gardeners by the name of "pitcher-plants" in the narrow sense.

The leaves in both the *Sarracenias* just named are heteromorphic. Some of them have acute linear-lanceolate petioles of a uniform green colour, and not hollowed out; and it is only in the case of from three to five leaves in each individual plant that the petioles are transformed into tubes with infundibuliform enlargements at the top. The rim round the mouth of the funnel is somewhat swollen and doubled down externally; but above the orifice the lamina is arched so as to form a cover to the pitcher. The margin of the leaf of *Sarracenia laciinata*, which is shown in fig. 21<sup>3</sup>, is crinkled and sinuously folded. The cover and also the upper funnel-shaped enlargement of the pitcher are very conspicuous on account of the contrast of the colours displayed upon them. The green of the lower part of the pitcher gets paler and paler above, and merges into a pure white, whilst dark-red veins stand out from the green and white ground tints, having the effect of a net-work of blood-vessels. At the mouth of the pitcher, and on the under side of the lid, honey is secreted in such abundance that little drops of it are not infrequently to be seen on the swollen rim, and some oozes down into the infundibuliform portion of the pitcher. But at the very spots where the honey occurs there are also innumerable smooth conical cells with their solid apices directed downwards; and these cells become longer the lower their position in the pitcher. When insects, attracted by the gay-coloured lid, and lured on by the honey, come to the mouth of the pitcher and tread upon the parts covered with the sharp slippery papillæ, they are drawn into the depths as though by an invisible power. After they have once alighted on the perilous area, every movement and every effort to climb up against the points causes them to slide further and further down towards the bottom of the pitcher, where they are hopelessly lost, being killed within a short time and ultimately decomposed.

An instance of an exactly similar kind is afforded by *Cephalotus follicularis*, which has long been known as a plant native on moorlands in eastern Australia. It is allied to saxifrages and currants, and is represented on a scale of half the

natural size in fig. 22. This *Cephalotus* also has two kinds of leaves, which are closely crowded in a rosette round the erect flower-stalk. Only the lower leaves of the rosette are transformed into traps for animals, and these are pre-eminently adapted for wingless creatures creeping upon the earth. The tankard-shaped traps all rest on the damp earth, and are furnished externally with borders or winged ridges, which facilitate the ascent of crawling animals to the mouth of the tankard. Flying insects are of course not excluded, and here again they are made aware from afar of the feast of honey provided by the presence of bright colours. The half-open lid is very prettily adorned with white patches and brilliant purple veins, and at a distance is readily mistaken for a flower.

When small animals, whether with or without wings, approach to take the honey, they are so eager in their search that they get upon the inner surface of the mouth of the tankard-pitcher, which, though fluted, is also very smooth and slippery, and thence they easily slide into the interior of the cavity. The pitchers being half-full of liquid, most of the unlucky creatures die there in a short time by drowning. But even if this were not the case they would never succeed in working their way up to the light of day. For every animal that wishes to save itself from a *Cephalotus* pitcher has three obstacles to overcome: first, a circular ridge projecting inside the pitcher; secondly, a bit of wall thickly covered with little papillæ, sharp, ridged, and pointed downward, the whole being comparable to a flax-comb; and, lastly, on the involute rim round the mouth of the pitcher, another fringe composed of hooked, decurved spines which bristle like an impenetrable row of bayonets in front of such animals as may have surmounted the other difficulties. The abundance of the booty found at the bottom of *Cephalotus* pitchers shows how efficiently these contrivances serve to prevent escape. Ants, for instance, sacrifice themselves recklessly in their pursuit of honey, and one often finds great numbers of them drowned in the liquid in the pitchers. The prey is not in this case converted into a putrid liquor, but is partially dissolved by a secretion having an acid reaction. This secretion is separated out by special



Fig. 22.—*Cephalotus follicularis*.

glandular cells situated on the lining of the pitcher; and the whole process, wherein they are concerned, corresponds to that which obtains in the pitchers of *Nepenthes*, and which will be more thoroughly discussed in the case of these latter plants.

The species of the genus *Nepenthes*, of which we know at the present time thirty-six, are all confined to the tropics. Their area of distribution extends from New Caledonia and New Guinea over tropical Australia to the Seychelles Islands and Madagascar, and over the Sunda Islands, the Philippines, Ceylon, Bengal, and Cochin-China. They only flourish on marshy ground on the margin of small collections of water in damp primeval forests. There the seeds germinate in shallow water. The young plants (see fig. 23),



Fig. 23.—Young *Nepenthes* plants.

which spring from the boggy ground, have their leaves arranged in rosettes just like those of *Sarracenia*s (see fig. 20). They are, too, so nearly identical in form with the latter that anyone seeing a young *Nepenthes* plant for the first time, and not knowing the history of its development, would take it for a *Sarracenia*. The leaves, succeeding the cotyledons and forming a circle

above them, rest their lower portions upon the mud, but their upper parts are curved upwards, and each carries at its extremity a scale resembling a cock's comb, which is, strict speaking, the lamina. This scale roofs over a slit-like aperture, the entrance to a cavity within the swollen petiole. In addition a green lobe with a few coarse projecting points is to be seen on either side of the orifice.

Altogether different from the rosettes of young *Nepenthes* plants are the foliar structures clothing the stems which subsequently arise from the rosettes (see fig. 24). In these leaves the lower part of the petiole is winged and flat, has a linear or lanceolate outline, and resembles the leaf-blade of *Dracaena*; its functions, too, are those of a green lamina. This expanded section of the leaf-stalk passes next into a part which is terete and coiled like a snake, and acts as a tendril. Every stem or branch belonging to a plant, whether living or dead, with which this part of the petiole comes into contact, is seized and encircled by it; and the third portion of the petiole, i.e. the pitcher, being situated at the extremity of this clasping portion, is thus slung upon the branch of some other plant growing at the edge of a pool of water. Meanwhile the *Nepenthes* plant rises higher and higher above the wet soil where its seeds germinated and the young rosette rested, becomes entangled with the ramifications of the underwood and with prostrate branches of trees of the primeval forest; in a word, with everything available as a support, and so not infrequently climbs, as a true liane, to the tops of trees of moderate height.

The pitcher must be looked upon as an excavated portion of the petiole, and

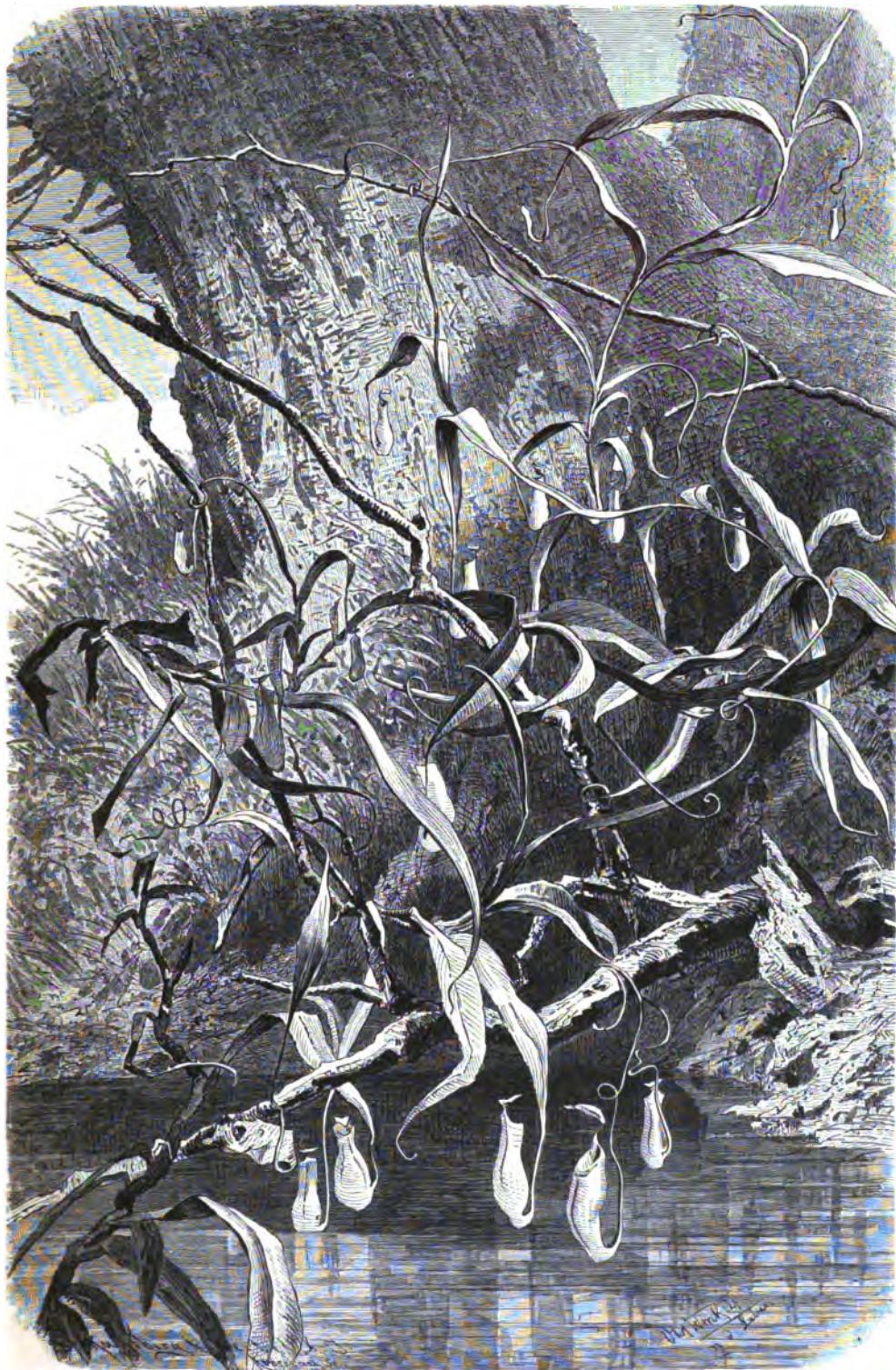


Fig. 24.—*Nepenthes distillatoria*.

what appears to be the lid of the pitcher is the lamina, as it is in *Cephalotus* and the *Sarracenias*. In this case also the lamina seems to be but little developed in comparison with the wonderfully metamorphosed petiole. In the majority of the species of *Nepenthes*, the mature pitchers are from 10 cm. to 15 cm. in height. In the graceful *Nepenthes ampullaria* they are only from 4 cm. to 6 cm. high; but, on the other hand, the species indigenous to the primeval forests of Borneo reach a height of 30 cm. or even half a meter. The pitchers of *Nepenthes Rajah* have a height of 50 cm., and their orifices are 10 cm. in diameter, whilst below the orifice they expand to 16 cm.; so that if a pigeon were to fly into a pitcher of this kind it would be completely hidden in it. Immature pitchers are still closed by their covers. Often they are hairy outside; and, according to the colour and lustre of the hairs, they may be rusty in tone or glittering like gold; not rarely they look as if they were powdered with flour (e.g. *N. albo-marginata*), and sometimes are even snow-white. Subsequently the lid is raised, and the downy coat disappears either partially or entirely. Having thus become glabrous, the pitchers display a yellowish-green ground colour, for the most part flecked and veined with purple; and many are of a bluish, violet, or rose tint near the orifice, or dark-red as though saturated with blood. The lid is similarly gaily coloured; and the variety of the tints is increased by the fact that a pale-blue zone is visible in the interior, beneath the swollen involute rim of the opening, which is itself brownish, yellowish, or orange-red. Gaily-coloured pitchers of this kind look at a distance just like flowers, and remind one, in particular, of the most brilliant floral forms of the liane-like *Aristolochias* indigenous to tropical forests. This fact is the more noteworthy, because the genus *Nepenthes* is closely allied to the genus *Aristolochia* in respect of systematic relations.

The bright pitchers of *Nepenthes*, visible from afar, are sought, just as flowers are, by insects, and probably by other winged creatures as well; and this occurs all the more because there is a copious secretion of honey by the epidermal cells upon the under surface of the lid, and on the rim round the mouth of each pitcher. The swollen and often delicately-fluted rim, in particular, drips and glitters with the sugary juice; and it would be permissible in this connection to speak of a honeyed mouth and sweet lips in the most literal sense of the words. Animals which suck honey from the lips of *Nepenthes* pitchers wander, as they do so, only too readily upon the interior surface of the orifice. But the inner face is smooth and precipitous, and rendered so slippery by a bluish coating of wax that not a few of the alighted guests slip down to the bottom of the pitcher and fall into the liquid there collected. Many of them perish in a short time; others try to save themselves by climbing up the internal face of the pitcher, but they always slip again on the polished, wax-coated zone, and tumble back once more to the bottom. In large pitchers the involute rim of the aperture is in addition armed with sharp teeth, which are pointed downwards and bristle in front of such of the unlucky victims in the pitfall as try to emerge (see fig. 19<sup>8</sup>). In a number of species (*N. Rafflesiana*, *N. echinostoma*, *N. Rajah*, *N. Edwardsiana*, and *N. Veitchii*, all

natives of Borneo) this fringe of sharp teeth looks like the set of teeth of a beast of prey; and in *Nepenthes villosa*, of which a pitcher is represented in fig. 21<sup>4</sup>, a double row of bigger and smaller teeth directed towards the bottom of the pitcher is developed, and renders the escape of prey, once caught in the trap, impossible.

Most of the creatures that fall into the pitchers are, however, speedily drowned in the large quantity of liquid at the bottom. For a third part or even a half of the cavity is filled with liquid. This liquid originates from special gland-cells on the inner surface of the pitcher, consists mainly of water, and so long as there are no animals in the pitfall, gives only a very weak acid reaction. But as soon as the body of an animal reaches the bottom, more fluid is secreted. This has a distinctly acid taste, possesses the power of dissolving albuminous substances, such as flesh and coagulated blood, and corresponds, not only in respect of this action but also in chemical composition, to the gastric juice. For, in addition to organic acids (malic, citric, and formic acids), an organic body like pepsin has been detected in it, and nitrogenous organic compounds have been brought into solution in it artificially as well. If the liquid from a *Nepenthes* pitcher, which has not yet captured any animal, is poured into a glass vessel containing a small piece of meat, the flesh is at first but little affected; but, if a few drops of formic acid are added, the flesh is dissolved and undergoes the very same changes as it does in the stomach of a mammal. The process going on in the pitchers of *Nepenthes* when animals fall into them is therefore not only analogous to digestion, but may be properly designated digestion.

The digested portions of the bodies are afterwards absorbed by special cells at the bottom, and on the lower parts of the lining wall of the *Nepenthes* pitchers.

The third group included in the first section of carnivorous plants comprises forms with scale-like leaves, within which are peculiar cavities penetrable by minute animals only, on account of the narrowness of the entry. Special contrivances to prevent the escape of the prey are absent. The animals are retained and drained of their juices in the cavities by means of protoplasmic filaments radiating from special cells.

One of the most remarkable of the plants belonging to this group is the Toothwort (*Lathraea Squamaria*), of which we shall repeatedly have occasion to speak. It is nearly allied to the Yellow-Rattle and Cow-wheat, but it is destitute of chlorophyll, and lives underground, parasitic on the roots of arborescent Angiosperms, except during a brief period annually when it sends up above-ground a few short shoots covered with flowers. The subterranean stems are white, have a fleshy, solid, and elastic appearance, and are covered throughout their entire length with thick squamous leaves placed closely one above the other (see fig. 25<sup>1</sup> and fig. 37). In colour and consistence these leaves are like the stem; in outline they are broadly cordate, and they give the impression of being mounted fairly and squarely upon the stem by means of the highly swollen and notched basal portion. But it is only necessary to detach one of the scales from the stem to convince oneself that this is not the case, and that the part taken at first sight to be the

underside or back of the leaf is only a portion of the superior surface. In reality each of these thick squamiform leaves is rolled back, and in it the following parts may be distinguished: first, the place of insertion on the stem (fig. 25<sup>3</sup>) which is relatively small; secondly, the portion taken on cursory examination to be the whole upper surface of the leaf, and consisting of an obliquely ascending blade limited by a sharp border; next, starting from this sharp border, the part, which, owing to its being suddenly bent down at an acute angle and falling away steeply, is usually taken for the dorsal or inferior surface of the leaf, but which belongs, in point of fact, to the front of the lamina; fourthly, the free extremity of the leaf in the form of an involute limb; and fifthly, the true dorsal part, which is very small relatively and is not visible until the involute tip is removed. Owing to the involution of the apex, a canal or rather a recess is formed and runs across beneath the leaf, close under the place where the latter is joined to the stem (see fig. 25<sup>2</sup>). From five to thirteen (usually ten) chambers open into these recesses through a series of little holes. They are excavations in the thickness of the scales and are probably, in this form at anyrate, unique in the realm of plants. These extraordinary chambers must be described as deep excavations in the foliar substance proceeding from the back of the leaf. To solve the problem of their significance in relation to the life of the plant, and to its absorption of nutriment in particular, it is necessary to examine them somewhat more in detail.

The cavities, varying in number, as has been already mentioned from five to thirteen, are situated very close together, but are not connected laterally. They are all deeper than they are broad, and have irregularly undulating walls (see fig. 25<sup>3</sup>). Two kinds of structures are conspicuous on the internal surfaces of the walls, being raised above the ordinary epidermal cells, and projecting into the cavity. Structures of the one kind are present in large numbers, and each of them consists of a pair of cells in the form of a little head, borne by a short, cylindrical cell serving as a stalk. The other variety, which occurs much more sparsely and is altogether wanting in the folds of the wavy inner wall, is composed of a comparatively large tabular cell, roundish or elliptical in outline, inserted amongst the ordinary epidermal cells and only slightly raised above them, and of two convex cells, forming a low dome, which rests upon this base (fig. 25<sup>4</sup>) as though on a salver. The walls of these cellular structures projecting into the cavity are comparatively thick, and when the protoplasts living in the cells are stimulated, they send out, through numerous pores in the thick walls, delicate filaments exactly like the protoplasmic threads which the coated Infusoria, known by the name of Rhizopoda, stretch forth through the pores of their armour (see fig. 25<sup>5</sup>).

When small animals penetrate into the labyrinthine chambers of a Toothwort leaf and touch the organs just described, the protoplasmic filaments are protruded in rays in response to the stimulus, and lay themselves upon the intruders. They act as prehensile arms in holding the smaller prey, chiefly Infusoria, and impede the motion of larger animals so as to cut off their retreat. No special secretion has been observed to be exuded in the foliar chambers of *Lathraea*. But, seeing that

some time after the creatures have entered the chambers the only remains of them that one meets with are claws, legs, bristles, and little amorphous lumps, their sarcode, flesh, and blood having vanished and left no trace, we must suppose that the absorption of nutriment from the dead prey here ensues through contact with the extended protoplasmic tentacular filaments as in the case of Rhizopoda, to

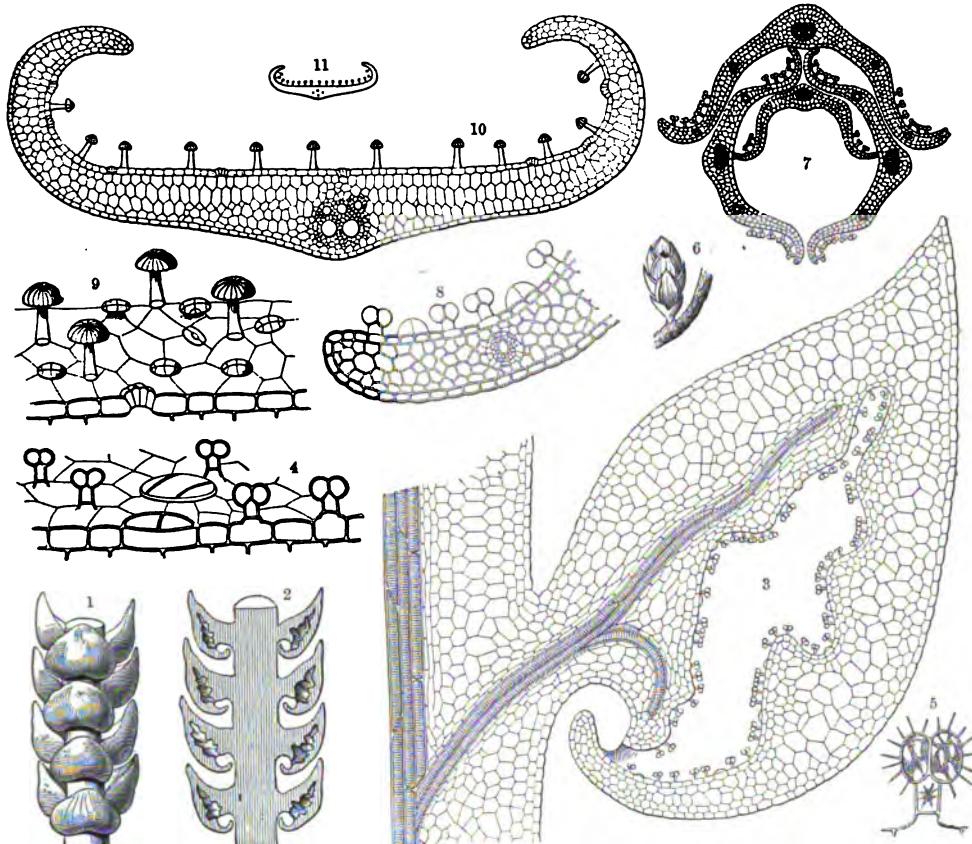


Fig. 25.—Capturing apparatus in the Toothwort, *Bartsia*, and Butterwort.

<sup>1</sup> Piece of an underground leaf-shoot of the Toothwort. <sup>2</sup> Longitudinal section through the same;  $\times 2$ . <sup>3</sup> Longitudinal section through a leaf;  $\times 60$ . <sup>4</sup> Piece of the wall of a cavity;  $\times 200$ . <sup>5</sup> Plasmic threads radiating from the cells of the little heads;  $\times 640$ . <sup>6</sup> Subterranean bud of *Bartsia*; natural size. <sup>7</sup> Cross-section through part of this bud;  $\times 60$ . <sup>8</sup> The margin of a bud-scale in section;  $\times 200$ . <sup>9</sup> Piece of the epidermis of a leaf of Butterwort;  $\times 180$ . <sup>10</sup> Transverse section through the leaf of a Butterwort (*Pinguicula alpina*);  $\times 50$ . <sup>11</sup> Transverse section through Butterwort leaf; natural size.

which these organs are so strikingly similar. It is not impossible that the sessile organs alone have the function of absorption, and that the stalked capitate structures serve for the retention of the prey; at least, this idea is supported by the circumstance that the former, which, as already stated, are much the scarcer, have vessels running to them connected by a peculiar barrel-shaped cell with the large elliptical tabular cells, and this is not the case with the capitate forms of structure.

The openings of the chambers into the recess at the back of a Toothwort leaf being very narrow, only minute animals, such as Infusoria, Amœbæ, Rhizopoda,

Rotifera, small Acarina, species of *Aphis*, Poduridæ, &c., slip in. What it is that prompts them to visit these hidden chambers is as hard to say as it is to give the reason why the various species of *Daphnia* and *Cyclops* make their way into the bladders of Utriculariæ. The most probable explanation is that the tiny creatures push into the cavities in their search for food, and there meet their death.

It has been already stated that *Lathraea* is a parasite. Although we shall not discuss the plant in that capacity until later on, we must point out now that the main part of its nutriment is derived from the roots of deciduous arborescent Angiosperms by means of special suckers. It only grows in regions where the activity of trees and shrubs is interrupted by a winter of considerable duration. As soon as the woody plants on whose roots individuals of *Lathraea* are parasitic acquire their autumn tints and shed their leaves, the suckers invariably perish. When, in the following spring, the ascent of the sap begins in the wood, *Lathraea* sends out new roots, which fasten their suckers underground upon the tree's roots, the latter being turgid with sap. The nutriment supplied in this way to *Lathraea* is not essentially different from that taken up by the roots of the tree or shrub in question from the surrounding earth. It is composed mainly of water holding a small quantity of mineral salts in solution, a mixture which has been termed not unsuitably "crude sap".

Living underground and being destitute of chlorophyll, *Lathraea* has not the power of converting atmospheric carbon dioxide, or crude food-sap absorbed by the suckers from the tree or shrub attacked, into the various organic compounds necessary for further growth. For this reason, and inasmuch as the quantity of nitrogenous compounds in the fluids withdrawn from the roots is but small, every additional supply of organic food, especially of nitrogenous matter, such as is derived from captured animals, must be exceedingly welcome. Although the prey that is caught and digested consists for the most part of minute Infusoria, this addition must not by any means be undervalued. We must take into account the fact that every one of the innumerable leaf-scales of an individual *Lathraea* has an apparatus for capture and digestion, and that this apparatus is active throughout the entire year. The frost in winter does not reach so deep down in the soil as the place where the plant is imbedded, so that there, even at a season when above-ground everything is quiescent, the Infusoria and other little organisms continue their existence and may be captured by *Lathraea*. Thus, the extremely large number of animals secured in the course of a year is nearly sufficient to maintain the size of each individual plant.

It is after all anything but strange that a root-parasite, destitute of chlorophyll and living underground, should make use of traps for animals, besides absorbing crude sap from other plants; but, on the other hand, we are naturally surprised to find plants which actually extract food from the earth by means of absorption-cells, also absorbing through suckers from roots in the capacity of parasites, and, furthermore, preying upon animals. An instance of such a plant is afforded, however, by *Bartsia alpina*. This remarkable organism is distributed in the

arctic region and amongst the high mountain flora throughout almost the whole of Europe, and is very striking owing to the colour of its foliage being a mixture of black, violet, and green. The flower, too, is of a sombre dark-violet hue, and the entire plant, by reason of this peculiar colouring, gives a truly funereal impression. We may remark incidentally that the name *Bartsia* was chosen by Linnaeus for this sad-hued plant as an expression of his own grief at the death of the zealous naturalist and physician, Bartsch, who was his intimate friend, and who succumbed at a comparatively early age to the climate of Guiana. Damp black earth in the neighbourhood of springs constitutes the favourite habitat of these plants. Upon digging in summer time down to their roots, one sees that a few suckers proceed from them, and fasten upon the sedges and other plants growing in the vicinity; but one also discovers subterranean shoots having "root-hairs" developed near the nodes, at which are inserted the paired white scales; and these "root-hairs" have the function of absorption-cells. Towards the autumn, oval buds, likewise subterranean, are matured, in form not unlike horse-chestnut buds (see fig. 25<sup>6</sup>), and composed of etiolated scales arranged in four rows and overlapping one another like tiles, so that only the back of the upper part of each scale is visible, the lower part being covered by the scale next beneath it.

On the visible part of each scale's convex under surface three sharply projecting ribs are noticeable near the middle, whilst the two margins are rolled back so as to form a recess in each case. But, as may be seen in the cross-section of a *Bartsia* bud (see fig. 25<sup>7</sup>), one pair of scales lies over the next higher pair in such a way as to convert the recesses into ducts. Owing to this construction the interior of the bud is perforated by twice as many ducts as there are covered leaf-scales, and the orifices of each pair of ducts occur at the spots where the evolute margins of one scale begin to be covered by the middle of the next lower scale. On one wall of the ducts, i.e. in the recesses, structures like those which occur in the cavities of *Lathrea* are developed, i.e. stalked glands, each composed of two cells borne upon a basal cell; secondly, pairs of hemispherical domed cells; and, lastly, ordinary flat epidermal cells (see fig. 25<sup>8</sup>). There can be little doubt that the whole apparatus acts in the same way as in *Lathrea*, and is adapted to the capture of Infusoria.

The subterranean buds of *Bartsia*, just described, are produced late in the summer, and aerial shoots arise from them in the course of the following spring; and seeing that the foliage-leaves on these shoots are richly furnished with chlorophyll, and manufacture organic compounds in the sunlight from the constituents of the air and from the fluids imbibed by absorption-cells from the ground, the question arises whether an additional supply of nutriment from the dead bodies of captured animals can be necessary or even advantageous. We shall, however, taking into account the circumstances of *Bartsia alpina* when growing wild, answer this question with an unconditional affirmative. The plant belongs, as has been said, to an arctic and high alpine flora, and grows in regions where the activity of plants above ground is limited to the short period of two months. After the lapse of this brief vegetative season, the aerial parts of arctic and alpine plants either

die altogether, or are buried in the snow, retaining their green colour, but suspending all movement and vital activity for from eight to ten months. The first snow falls in the districts inhabited by *Bartsia* invariably before the ground is frozen, and the wintry covering of snow, which gets deeper and deeper as time goes on, protects the earth so completely from the cold that even in the superficial strata the temperature does not sink below freezing point. In the bed thus kept free from frost neither vegetable nor animal life is quite torpid, and there can be no doubt that it is only beneficial to *Bartsia*, during the long interval, for its subterranean buds to obtain an abundance of food from the bodies of captured Infusoria. The advantage is the more obvious when one considers that the above-ground stem, with its foliage-leaves and flowers, has to be built up in two or three weeks, in the ensuing vegetative period, from the organic compounds stored in the cells of the scales of the subterranean buds, and that both the damp ground in which *Bartsia* grows, and also the roots of the marsh-plants to which it is joined by a few suckers, though yielding water and mineral salts, afford but little material for the production of nitrogenous compounds.

#### CARNIVOROUS PLANTS WHICH EXHIBIT MOVEMENTS IN THE CAPTURE OF PREY.

We have taken *Lathraea* and *Bartsia* as types of the last group of that section of carnivorous plants which manifest no external visible movement in the pitfalls for the purpose of capture or digestion. The second section, now to be discussed, includes plants in which movements of the leaves, or parts of leaves, modified as organs of seizure and digestion, take place as a result of the contact of animal bodies—movements which have the common object of bringing about the digestion of the animals, whilst the retention of the latter is effected in very various ways.

Since in *Lathraea* and *Bartsia* the leaves, modified as organs of capture, exhibit no kind of motion themselves, though movements take place in the protoplasm of the capitate pairs of cells in the interior of the cavities, having as their object the holding of the prey, these plants form, to a certain extent, a link between the first and second sections. All these divisions are for that matter merely artificial, and it is not impossible that fresh forms may be discovered and recognized as intermediate between the groups and series here distinguished, obliterating the boundaries which have been adopted by us, simply with a view to obtaining a general survey of the subject.

The first group of carnivorous plants which perform movements for the capture of prey is composed of the various species of the genus *Pinguicula* (Butterwort). Of this stock nearly forty species are known; and they are all much alike. Scarcely any difference would be detected by an ordinary person between *Pinguicula calyprata* from the mountains of New Granada and *Pinguicula vulgaris* from our own hills. In respect of habitat, too, they exhibit close conformity. In both the Old World and the New they only thrive on damp spots, the neighbourhood of

springs, banks of brooks, moorlands, and black peat-bogs. In the equatorial zone they have retired into the cool regions of the higher mountains. The mountain ranges of Mexico are particularly rich in species of *Pinguicula*, but all the forms existing there occupy a circumscribed area. Southern and western Europe also harbour a few native species whose area of distribution is surprisingly limited. The species occurring in the arctic and sub-arctic zones are, on the contrary, exceedingly widely distributed. One species has been found in antarctic regions at the Straits of Magellan.

The species best known and most available for study is *Pinguicula vulgaris*. The area of its distribution extends over the whole of the arctic and sub-arctic regions, over the part of North America which lies to the north of the Mackenzie River, over Labrador, Greenland, Iceland, and Lapland, throughout Siberia down to the Baikal Mountains, and through Europe to the Balkans, Southern Alps, and Pyrenees. This graceful plant is represented on its natural scale and growing on a bog in the annexed Plate II. entitled, "Insectivorous Plants: Sun-dew and Butterwort". It has bilabiate flowers of a violet-blue colour, with palates covered with velvety-white hairs, and with a sharp spur at the back. The flowers are borne singly on slender stalks which rear themselves in an elegant curve from the centre of a rosette of leaves that rests upon the ground. The leaves of the rosette in *Pinguicula vulgaris*, as in all other species of Butterwort, are oblong-ovate or ligulate and of a yellowish-green colour, and rest their under-surfaces upon the wet ground, whilst their upper faces are exposed to the sky and rain. Owing to the lateral margins being somewhat upturned, each leaf is converted into a broad flat-bottomed trough (cf. the section taken right across a leaf in fig. 25<sup>10</sup> and 25<sup>11</sup>). The trough is covered with a colourless sticky mucilage which is secreted by glands distributed in large numbers over the entire upper surface of the leaf.

The glands are of two kinds. One variety is distinguishable by the naked eye as consisting of a stalked head, and looks under the microscope like a tiny mushroom (see fig. 25<sup>9</sup>). Its parts are a swollen disc composed of from eight to sixteen cells grouped radially, and a stalk, consisting of an erect tubular cell supporting this disc. A gland of the other sort is made up of eight cells grouped in the form of a wart or knob supported by a very short stalk-cell, and only slightly raised above the surface of the leaf. For the rest, ordinary flat epidermal cells make up the epidermis, with here and there interspersed the guard-cells of stomata.

It has been calculated that there are 25,000 mucilage-secreting glands on a square centimeter of a butterwort leaf, and that a rosette composed of from six to nine leaves bears about half a million of them. Momentary contact, whether due to rapid brushing by a solid body or to the incidence of drops of rain, causes no kind of movement in them. The long-continued pressure of grains of sand or of solid insoluble bodies in general stimulates the glandular cells to an inconsiderable augmentation of the quantity of mucilage discharged, but does not cause secretion of any acid digestive fluid. But as soon as a nitrogenous organic body is brought into continuous contact with the glands, they are forthwith stimulated not only to

a more profuse elimination of mucilage, but also to the secretion of an acid liquid, which has the power of dissolving all bodies of the kind, namely, such as clotted blood, milk, albumen, and even cartilage. It has been experimentally established (for example) that small solid bits of cartilage placed on a leaf of *Pinguicula vulgaris*, whose mucilage shows no sign of an acid reaction, cause, after ten or eleven hours, the secretion of an acid liquid, and after forty-eight hours are almost entirely dissolved by it. At the end of eighty-two hours the bits of cartilage used in the experiment were completely liquefied, the whole secretion was reabsorbed, and the glands had become dry. When small insects such as midges alight from flight on a leaf of *Pinguicula* they remain glued by the mucilage, and their struggles to extricate themselves only cause them to sink deeper into it. Thus they generally perish in a very short time, are digested by the acid juice poured from the glands in response to the stimulus, and are absorbed with the exception of the wings, claws, and other parts of the skeleton.

The acid liquid secreted by the glands is viscous, and when a number of glands are irritated it may exude so copiously as to fill the whole trough of the leaf. If the margin of the leaf alone is stimulated, as when a small creeping insect, or a midge alighting from above, gets upon the slightly up-curved margin of the leaf, not only do the marginal glands, which are comparatively infrequent, discharge their secretion, but in addition the edge curls over; the object of this movement being to cover, if possible, the prey whilst it is held fast by the sticky mucilage, or to push it into the middle of the flat channel, and so, in one way or the other, to bring it into contact with as many glands as possible. The marginal glands alone would not produce the requisite quantity of acid liquid to effect solution, and, on this account, the glands on a wider area are summoned to assist in the manner described. The involution of the margin takes place very slowly; it is usually some hours before the animal sticking to the edge is enfolded, or, in the case of the larger specimens, is pushed into the middle of the leaf. After solution and absorption are accomplished, usually by the end of twenty-four hours, the leaf expands again, and its margins assume the position which they had before their involution.

Besides small insects, pieces of plants, such as spores and pollen-grains brought by the wind, not infrequently fall on the viscid surfaces of *Pinguicula* leaves. These are subjected to the same fate as animal organisms; their protoplasts being dissolved and absorbed like the flesh and blood of insects.

The action of the acid juice secreted by the glands of butterwort leaves upon albuminous bodies is identical with that of the gastric juice of animals. We may presume therefore that there are in it, as in the gastric juice, two kinds of substance: firstly, a free acid, and, secondly, a ferment completely analogous to pepsin in its action; for, as is well known, it is by means of this combination that the juice of the animal stomach effects the solution of albuminoid compounds. Inasmuch as the gland-cells of *Pinguicula* absorb all the soluble part of the prey, and re-absorb the solvent previously discharged by them, the action of this plant's leaves

PLATE II.



1. *Drosophyllum lusitanicum*.

2. *Pinguicula vulgaris*.

3. *Sphagnum cymbifolium*.



PLATE II.



INSECTIVOROUS PLANTS: SUNDEW AND BUTTERWORT.



is exceedingly like that of the animal stomach, and the process may, as in the case of *Nepenthes*, be fairly regarded as digestion. Whether, in carrying out this process, the different forms of glands have also different functions, whether those of one kind serve principally to secrete and those of the other to absorb, or whether, perhaps, the one variety only discharges viscid mucilage to capture the prey, and the other only a liquid containing acid and pepsin, are questions not yet determined with certainty, although such a division of labour is in itself highly probable.

The similarity existing between the leaf of *Pinguicula* and the animal stomach in respect of their action on albuminous substances was turned to a practical application in dairy-farming long before the discovery of the relationship by men of science. The very same changes as are brought about in milk by the addition of the rennet from a calf's stomach can be induced by means of butterwort leaves. If fresh milk, warm from the cow, is poured over these leaves, a peculiar tough mass of close consistence is formed, the "Tätmiölk" or "Sätmiölk" of Laplanders, mentioned by Linnæus a hundred and fifty years ago as constituting a very favourite dish in northern Scandinavia. In particular, the fact that by means of a trifling quantity of Tätmiölk, produced in the manner described, a large amount of fresh sweet milk may be also converted into Tätmiölk is specially worthy of emphasis, for we learn from it that the substance generated by *Pinguicula* behaves in this respect too, like other ferments. The immemorial use of *Pinguicula* leaves by shepherds in the Alps as a cure for sores on the udders of milch cows is also interesting, inasmuch as the curative effect on the sores is to be explained by the antiseptic action of the secretion of the leaves in question, and a method of healing, used empirically two centuries ago, thus finds confirmation and a scientific explanation at the present day.

Since the curling up and unrolling of the leaf-margin in butterwort is accomplished but slowly, the process above described is not at all conspicuous. Moreover, the margin of a young leaf is always incurved, and that of a mature leaf is also somewhat turned up before stimulation has taken place; so that, strictly speaking, we only have to do with a greater or smaller degree of involution, and its nature can only be determined by careful observation.

In the plants which form the second group in this section of carnivorous plants, and of which the best known representatives are the various species of the genus Sun-dew (*Drosera*), the movements, whereby the capture and digestion of small animals is effected, occur much more rapidly and obviously. These species are usually rooted in the damp dark soil of moors. They have also the same habitats as *Pinguiculae*, and often enough sun-dew and butterwort are to be seen flourishing close together on a strip of boggy ground no larger than one's hand. On Plate II. they are shown thus associated. *Drosera rotundifolia*, together with *Pinguicula vulgaris*, is there represented, life size, growing in a bed of sphagnum amongst sedges on an upland moor. The thing that strikes one most at sight of the round-leaved sun-dew depicted, and in general of all the forty known

species of *Drosera*, is the presence of the delicate wine-red filaments, clavate at their free ends and each supporting a glistening droplet of fluid, which stand out from the leaves, and whose function is essentially the same as that of the glands, stalked and sessile, on the leaf of *Pinguicula*. These filaments only proceed from the upper surface and margin of the sun-dew leaf. The under surface is smooth and hairless, and in many species, including the *Drosera rotundifolia* depicted on the plate, it rests upon the damp mossy ground. In this particular, and also in the circumstance that all the leaves of each individual are adpressed to the ground and grouped in a rosette or radially around the central slender flowering-stem, there exists a very obvious analogy between *Drosera*, and not *Pinguicula* alone, but many other carnivorous plants, such as *Sarracenia*, *Heliamphora*, *Cephaelotus*, and *Dionaea*, the fly-trap presently to be described.

The filaments or tentacles projecting from the upper surface and margin of the leaf look like pins inserted in a flat cushion and are of unequal size. Those which stand up perpendicularly from the middle are the shortest, and those which radiate from the outermost edge are the longest (see fig. 26<sup>4</sup>). Between these extremes are intermediate lengths gradually leading from the one to the other. There are on a leaf, in round numbers, about two hundred of these tentacles. The clavate head at the free extremity of each must be regarded as a gland. It secretes a clear, thick, sticky matter which is readily drawn out into threads, and which shines and glitters in the sunlight like a drop of dew, whence the plant has derived its name of sun-dew. Shocks occasioned by wind or the dropping of rain do not excite any kind of movement in the tentacles. If grains of sand are blown upon them by the wind, or if little bits of glass, coal, gum, or sugar, or minute quantities of paste, wine, tea, or any other non-nitrogenous substance are brought by artificial means into contact with the enlarged extremities of the tentacles, the exudation of liquid at the places in question is augmented, and the secretion also becomes acid, but there is no elimination of pepsin, and no change of importance ensues in the direction of the tentacles, or the attitude of the leaf-margin. But the moment a small insect, mistaking the glittering drops on the tentacles for honey as it flies by, alights on the leaf and so touches the glands, or upon the artificial placing of particles of nitrogenous organic matter, such as flesh or albumen, on the tentacle-heads, there ensues, as in the case of *Pinguicula*, an increase in the discharge of acid juice, as well as the addition of a ferment to its composition. The action of this ferment on albuminous compounds is entirely similar to that of pepsin, and we may even go so far as to speak of it as pepsin.

The insects that fly on to the leaves and are caught by the sticky juice try to disencumber themselves by stroking the viscous matter off with their legs, but they only besmear themselves still more, and are soon plastered all over the body, and have their movements greatly impeded by the secretion. Their efforts to save themselves soon cease, the orifices of their respiratory organs are covered with the juice and choked, and after a brief interval they die from suffocation. All these phenomena correspond, in the main, to those occasioned by identical causes in the

case of *Pinguicula*. But the leaves of the sun-dew are especially characterized by the movements performed by the tentacles in response to stimulation by animal matter. These movements are exhibited most conspicuously by the longest tentacles, which stand out radially from the edge of a leaf. A few minutes after the gland of one of these marginal tentacles has been excited by a living or dead animal becoming glued to it, a systematic disturbance is set up in the whole fringe of tentacles. First, the tentacle bearing the gland originally irritated with the animal's body attached to it, bends inwards, performing a movement similar to that

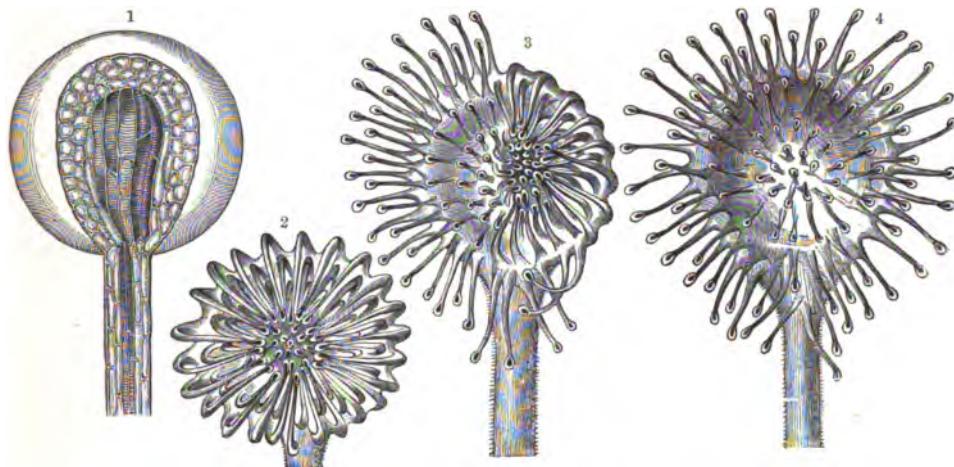


Fig. 26.—Tentacles on leaf of Sun-dew.

<sup>1</sup> Glands at the extremity of a tentacle;  $\times 80$ . <sup>2</sup> Leaf with all its tentacles inflexed towards the middle. <sup>3</sup> Leaf with half the tentacles inflexed over a captured insect. <sup>4</sup> Leaf with all the tentacles extended. Figs. 2, 3, and 4  $\times 4$ .

of the hand of a watch. Under peculiarly favourable circumstances it describes an angle of  $45^\circ$  in from two to three minutes, and an angle of  $90^\circ$  in ten minutes. A still more intelligible comparison than that of the hand of a watch is afforded by the human hand. Supposing that the foreign body is glued to the tip of a finger it would be moved by the curvature of the finger to the palm in the course of ten minutes. About ten minutes after the first tentacle has been set in motion, those standing near it begin to bend also (see fig. 26<sup>3</sup>). After another ten minutes, tentacles situated further off follow suit; and in the course of from one to three hours all the tentacles are inflected and converge upon the body in question.

We must not omit to mention that this object does not always occupy the same place on the surface of the leaf. Often, no doubt, the prey is exactly in the middle, and the tentacles then swoop down one after the other to that spot; but often also the place is elsewhere and yet the movements never fail in their aim. It may happen that a median tentacle, on repeated excitation, may have to bend now to the right, now to the left. When little bits of meat are placed simultaneously on the right and left halves of the same sun-dew leaf, the two hundred tentacles divide into two groups, and each one of the groups directs its aim to one of the bits of meat. This happens also if two small insects alight at the same moment on a leaf,

one on one side and the other on the other. The movement of the tentacles is often accompanied by an inflection of the whole surface of the leaf, the lamina becoming concave like a hollow palm, and when, under these circumstances, the tentacles have converged from the margin on to the concave central part, the leaf has the effect of a closed fist (see fig. 26<sup>2</sup>).

All these movements vary from one case to another and supplement one another according to the needs of the moment and with a view to immediate advantage. The one result that is always attained by the combined action is the covering of the prey with a copious supply of the secretion poured from a number of glands, so that it is dissolved and rendered fit for absorption and for the purpose of nourishment. When an insect is caught by one of the marginal tentacles, the secretion there discharged would not suffice for these purposes. The prey is accordingly transported as far as possible towards the middle of the lamina, where it comes into contact with the digestive juice exuded from a maximum number of glands. It is only when the size of the animal is rather large that the leaf becomes hollow in the middle like a spoon, with the juice of more than fifty glands concentrated in the depression. In a case of this kind the tentacles continue inflexed much longer, because the solution of the prey requires more time. If the captive is very small, its solution and absorption are completed in a couple of days. Afterwards, the tentacles lift, straighten themselves, and resume their original positions. The jaws, wings, compound eyes, leg-bones, claws, &c., of the captured animals are left behind undigested; but the flesh and blood are totally absorbed, and the liquid poured out by the glands to effect solution is also re-imbibed by them. The undigested remnants being now suspended on dry tentacles are easily blown away from the sun-dew leaves by the wind. After an interval of a day or two the glands at the ends of the tentacles, now occupying their original positions, again separate out a viscid fluid in the form of tiny dewdrops, and the leaf is once more furnished with the means of securing insects, and is able to repeat the movements above described.

Amongst the animals which fall victims to the sun-dew the most predominant are little midges; but rather larger flies, too, ants both with and without wings, beetles, small butterflies, and even dragon-flies, as they run, creep, or fly past, adhere to the extended gland-bearing tentacles as though they were lime-twigs. The larger animals, such as dragon-flies, are secured by the co-operation of two or three adjacent leaves. Some idea of the large number of captives made by a sun-dew is given by the fact that once upon a single leaf were found the remains of thirteen different insects.

In order to place in a true light the vast significance of the movements of the tentacles belonging to *Drosera* leaves in relation, not only to the nourishment of that plant, but to plant-life in general, it is necessary to direct attention to the facts that these movements are accomplished not in the cell directly excited, but in others, i.e. in adjacent cells belonging to the same community; that a propagation of the stimulus takes place from one protoplast to a second, thence to a third, fourth,

tenth, and so on, to a hundredth, and that the speed of transmission is susceptible of measurement. The movements occasioned in protoplasts situated at a distance from the seat of irritation by the stimulus propagated from its vicinity are, according to the position of the stimulating object, sometimes in one direction, sometimes in another, but in every case they are purposeful and for the benefit of the whole organism.

Investigations with a view to determining the degree of sensitiveness of *Drosera* leaves yielded the following results. A particle of a woman's hair, 0·2 mm. long and weighing 0·000822 mg., when placed upon a gland of *Drosera rotundifolia*, caused a movement of the tentacle belonging to the excited gland, which manifested itself externally as an inflection. If so minute a body of the kind is placed on the human tongue, its presence is not perceived, so that the sensitiveness of the protoplasts in the glands of the sun-dew is greater than that of the nerve extremities in the tip of the tongue, though the latter are well known to be the most sensitive in the human body. A four-thousandth part of a milligram of ammonium carbonate sufficed to induce motion, as also did  $\frac{1}{5000}$  mg. of ammonium phosphate. It would lead us too far to consider all the experiments in detail, but they point to the conclusion that liquid substances stimulate more strongly than solid bodies, and that the more nutritious to the plant the material placed upon the gland, the more quickly does the inflection of the tentacles ensue.

The propagation or conduction of a stimulus from cell to cell, as it takes place in the cell-community constituting a sun-dew leaf, may be compared to the conduction of stimulus by nerves from a sense-organ to the central organ, and of the force of will from the brain to the muscles. This transmission is conceived to be a progressive movement affecting the ultimate particles of the nerves, and comparable to the conduction of sound, light, and electricity; but no one has yet succeeded in making these movements visible. So much the more interesting is it to be able to see and follow in the glands and tentacles, by the aid of very slight magnifying power or even with the naked eye, the material change which occurs in the protoplasts of the sun-dew leaf when they are receiving or transmitting a stimulus. The pedicel of a tentacle is penetrated by one or two vessels with fine spiral sculpturing on the inner surface, and around these are parenchymatous cells. The gland has in the middle a group of oblong cells sculptured internally with very delicate spiral thickenings ("spiroids"), and the vessel or pair of vessels running down the middle of the tentacle (see fig. 26<sup>1</sup>) merge into these spiroids. A parenchyma composed of two or three layers surrounds the median group of spiroids. In each parenchymatous cell the protoplast is discerned forming a thick lining to the wall, and having a continuous streaming motion: whilst within the vacuole is contained a homogeneous liquid of a purple colour. If the minutest fragment of animal matter, such as flesh or albumen, be placed on these cells it acts as a stimulant on the contents of the cell-cavities, and the impulse manifests itself in a division of the hitherto homogeneous purple liquid into dark, roundish, club-shaped and vermiform lumps, cloudy spheres, and an almost colourless liquid.

This change, known as "aggregation", is propagated from the spot irritated down from one cell to another through the tentacle, across the leaf surface to adjoining tentacles, up to the heads of these, and so further and further radiating, so to speak, in all directions. Accompanying this visible sign of conduction, we have the bending of all tentacles in which the purple fluid is altered in the way described. When the source of excitation, the piece of flesh, is dissolved and digested, and the tentacles resume their original position, the dark lumps and spheres in the cavities



Fig. 27.—Venus's Fly-trap (*Dionaea muscipula*).

of the protoplasts disappear, and the homogeneous purple colour is restored as it existed before the stimulation.

The various species of the Sun-dew genus are distributed over all parts of the world, and are more numerous than those of any other genus of the family of Droseraceæ. Most of the other genera belonging to this order (*Dionaea*, *Aldrovandia*, *Byblis*, *Roridula*, *Drosophyllum*) are by no means rich in members. Each is represented merely by a single or few species, and is found exclusively in a very limited district. Like *Drosera*, they are all insectivorous plants, and all have the power of dissolving, absorbing, and using as supplementary nutrient, nitrogenous compounds from dead animals. The most striking of them are *Dionaea* and *Aldrovandia*. They form the very small third group of animal-captors, in which movements are performed for the purpose of prey, and their apparatus for

seizure and digestion is one of the most curious adaptations displayed by the vegetable world.

The Venus's Fly-trap (*Dionaea muscipula*), which is represented above (fig. 27), half its natural size, grows wild only in a narrow strip of country in the east of North America (from Long Island to Florida) in the vicinity of peat-bogs. The leaves, like those of many other carnivorous plants, are grouped in rosettes round the flowering axes, and for the most part rest their under surfaces either entirely or partially upon the ground. Each leaf consists, first, of a flat, spatulate petiole, which is, as it were, truncated in front and suddenly contracted to the midrib, and, secondly, of a roundish lamina. The latter is divided by the midrib into two symmetrical halves, inclined to one another at an angle of from  $60^{\circ}$  to  $90^{\circ}$  like the leaves of a half-open book. Both margins of the lamina run out into from twelve to twenty long, sharp teeth, which, however, do not carry either glands or any other special structures on their tips.

On the central part of each half of the leaf there are three very stiff and sharp spines, which are always shorter than the marginal teeth, and which stand up obliquely. They are composed of elongated cells whose protoplasm throughout life is in very active circulation. At the base of each spinous process is a short cylindrical pad of tissue formed of small parenchymatous cells, and this pad allows the spine to be deflected. The spines themselves are rigid, and do not bend in response to pressure, but are forced down on to the surface of the leaf, the pad of tissue referred to acting as a hinge. In addition to these processes, glands are scattered over the whole upper surface of the lamina. They look like the shortly-stalked glands of a butterwort leaf, are composed of some twenty-eight small cells, are purple in colour, and capable of secreting a mucilaginous liquid. Little trichomes, stellate hairs, are also borne on the edge of the leaf between the sharp teeth and also on the under-surface.

No visible change is produced by a blow or shock or by pressure affecting the whole plant or leaf, as might be caused by wind or falling drops of rain, nor even by injuries to the petiole or back of the lamina. But as soon as the upper surface of the lamina is touched, the two lobes, hitherto at right angles, approach one another until the sharp marginal teeth are interlocked, and the body touching the leaf is inclosed between two walls (fig. 28<sup>2</sup>). When the places beset with purple glands are alone excited by contact with the object, this inflection and closing follows very slowly; but if one of the six spines projecting in trios from the two foliar lobes is ever so lightly touched, the leaf shuts up within 10–30 seconds, i.e. instantaneously, and the action is best compared to the slamming of a half-open book. The teeth standing at the edge of the leaf lock into one another on these occasions like the fingers of clasped hands. The lobes, however, whose surfaces were hitherto plane, become at the moment of closing somewhat concave, so that when approached they do not lie flat against one another but inclose a cavity, the contour of which nearly corresponds with that of a bean.

The further changes and processes now ensuing depend upon whether the

sensitive part of the leaf was subjected to prolonged or only momentary contact, and also upon the nature of the body touching it, whether inorganic or organic, non-nitrogenous or nitrogenous. When rapidly touched or stroked, the leaf folds together, but only remains closed for a short time. The lobes soon begin to re-open, and can be stimulated afresh immediately and caused to shut again. This is also the case when the disturbance was due to the impact of a grain of sand or any other inorganic body, and likewise when the stimulus proceeded from an organic but non-nitrogenous object. But if, on the other hand, the body upon the upper surface of the lamina was nitrogenous and the contact not too hasty, the two lobes of the leaf remain closed over the object for a longer period. They also

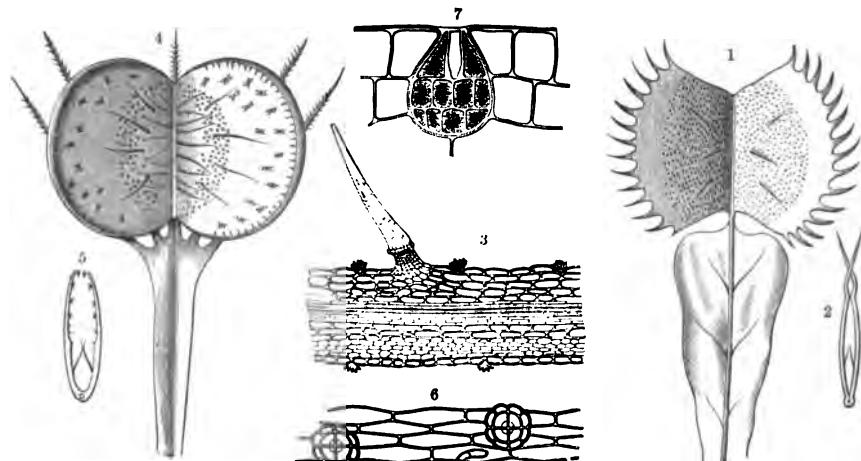


Fig. 28.—Capturing apparatus of the leaves of *Aldrovandia* and *Venus's Fly-trap*.

<sup>1</sup> Expanded leaf of a *Venus's Fly-trap*. <sup>2</sup> Section of a closed leaf. <sup>3</sup> One of the sensitive bristles on the surface of the leaf. <sup>4</sup> Expanded leaf of *Aldrovandia*. <sup>5</sup> Section of a closed leaf. <sup>6</sup> Glands on the surface of leaf of *Aldrovandia*. <sup>7</sup> Gland from the wall of a *Sarracenia* pitcher.

become flat and even again, and are pressed together so tightly that intervening bodies, if soft, are squeezed and crushed to pieces. In addition, the glands, dry till then, begin to secrete a slimy, colourless, highly acid juice; and this is true even of those glands which are not at all in contact with the nitrogenous bodies inclosed. The secretion flows so copiously that it can be seen in the form of drops if the shut lobes be forcibly separated. It covers the imprisoned body and gradually dissolves the albuminous compounds therein contained. Afterwards, the secretion and the matter dissolved in it are re-absorbed by the same glands as previously discharged the acid liquid, containing pepsin, in response to the stimulus; and when the trap reopens, the glands are dry. The soluble part of the prey has now vanished: the six little spinous processes, which were bent in the closed leaf like the blades of a pocket-knife and lay pressed down upon the surface, stand up; and the leaf is once more equipped for making fresh captures.

The time requisite for the digestion of a nitrogenous body, resting upon the surface of a leaf, varies according to the size of the body. The leaf usually remains closed for from eight to fourteen days, but often even for twenty days. Although

the larger live articulated animals—earwigs, millipedes, and dragon-flies—caught upon the upper surface of the leaf, cause the lobes to slam together, they are able to slip out if part of their bodies projects beyond the toothed margin, for the teeth are flexible and yield to strong pressure. But small creatures are hopelessly lost when the lobes have closed over them. They are at once suffocated in the liquid, which is poured out copiously by the glands, and are then dissolved and absorbed with the exception of their claws, leg-bones, chitinous rings, &c., which are incapable of being digested.

In spite of the identity of aim and of result, the mechanism of a *Dionaea* leaf differs very materially from that of the sun-dew leaf described above. Division of labour is carried much further in the Fly-trap. The pre-eminently sensitive structures, viz., the six filaments situated upon the upper surface of the leaf,



Fig. 29.—*Aldrovanda vesiculosa*.

do not act also as digestive glands. Again, the long sharp teeth at the edge of the leaf, which correspond in position to the marginal tentacles of a sun-dew leaf, carry no glands, and only serve to close the trap securely when an animal has been caught. Accordingly in *Dionaea* there exist special structures for three different functions, namely, stimulation, seizure, and digestion, whilst in the case of *Drosera* all these functions belong to the gland-bearing tentacles alone. The stimulus acting on the sensitive filaments on the leaf of the Fly-trap is liberated in the form of a rapid motion of the lobes and a discharge of digestive fluid from the glands, and this discharge of secretion ensues therefore through the mediation of cells which have not themselves been directly excited. The process here again is much more striking than in the sun-dew leaf. The transmission of stimulus, though as a fact identical in the two plants we are comparing, proceeds at any rate with much greater rapidity in *Dionaea* than in *Drosera*.

The analogy existing between these processes, especially the conduction and liberation of stimulus, and similar phenomena of the muscles and nerves in an animal organism, has already been brought out in discussing the sun-dew. It is a noteworthy fact that, in the fly-traps, actual electric currents have been observed, which prove that the greatest resemblance exists to muscles and nerves as regards electro-motor action also. A positive current runs from the base to the apex of the lamina; another current running in the opposite direction is demonstrable in the petiole; and the upper layers of cells in the lamina and the midrib are ascertained

to be the seat of origin of this phenomenon. A great alteration in the intensity of the current ensues upon each excitation of the leaf; and, inasmuch as this fluctuation of the electric current precedes the movement of the leaf caused by the stimulus, it is natural to assume that it depends upon the conduction and liberation of the stimulus.

*Aldrovandia*, the plant nearest allied to the Fly-trap in the structure of its leaf, is a water-plant, which occurs scattered over the southern and central parts of Europe. It only flourishes in shallow ditches, pools, and small ponds inclosed by banks of reeds and rushes, where the plants are immersed in clear, so-called soft water, attaining in summer to a temperature of 30° C., and are exempt from any incrustation of carbonate of lime, whereby the tender parts of the leaves might be hindered in their movements. On cursory inspection, one might take *Aldrovandia vesiculosa*, which is represented above full size and in its natural position, for a *Utricularia* (cf. fig. 17). It lives, like the latter, floating in water; is destitute of roots, and has a slender filiform stem with leaves arranged in whorls and terminating in bristles. In proportion as it grows at the apex, the hinder part dies away and decays. The development of hibernating buds takes place also in precisely the same manner as in *Utricularia*. Towards autumn, the stem ceases to elongate, and the two hundred small and young leaves, which adorn the extremity of the stem and whose cells are quite full of starch, remain lying closely wrapped one upon another and form a dark, oval, bristly ball, which sinks at the commencement of winter to the bottom of the pool or pond and hibernates there lying upon the mud.

It is not till very late in the following spring, when little midge-larvæ and other animals begin to move about in the water, that fresh life is awakened in these structures. The starch-grains in the leaves are brought into solution and used for building-material; the axis elongates, and lacunæ filled with air are developed, whereupon the plant becomes lighter, ascends, and remains throughout the summer and autumn floating just below the surface of the water. Although the little leaves of the winter-buds generally admit of the recognition of their future form, the apparatus adapted to the capture of animals is but little developed on them. But when once the leaves are mature, they bear laminæ, which are extremely like those of *Dionaea* in shape, and serve, as do the latter, for the capture of small animals. Each leaf is differentiated, as in *Dionaea*, into a strong, dark-green petiole expanded and anteriorly clavate, and into a roundish lamina with a delicate epidermis and with two lobes connected by the midrib and inclined nearly at right angles to one another (see fig. 28<sup>4</sup>). The midrib projects beyond the apex of the delicate lamina in the form of a bristle. In addition, comparatively long, rigid bristles, tipped with extremely fine spines, proceed from the petiole close to where the latter is joined to the lamina; and these bristles, which are directed forwards, give the whole leaf-structure a spiky appearance and prevent the approach of such animals as are not suitable for prey. The two margins of the lamina are bent inwards, and their rims are studded with small conical points. On the surface of

the lamina, especially along the midrib, there are pointed hairs; and a great number of glands, some larger and some smaller, occur from the midrib to nearly the middle of each lobe. The larger glands are discoid, and not unlike the sessile glands on the leaves of *Pinguicula*. They consist of four median cells with twelve others grouped in a circle round them, and are borne upon a very short stalk. The small glands are few-celled, being usually composed simply of a capitate-cell resting upon a short foot-cell (see fig. 28<sup>4</sup>). Towards the incurved margin of the lamina are displayed scattered stellate hairs, i.e. groups of cells so arranged as to present the appearance of a St. Andrew's cross when seen from above.

If minute animals or Diatomaceæ, especially species of *Navicula*, whilst swimming about in the water, touch the upper surfaces of the lobes set at right-angles—in particular, if the hairs in the middle are stroked as they creep by—the two lobes shut together quickly in the same way as those of *Dionaea*, and the animal or *Navicula*, as the case may be, is then enclosed in a cage between two somewhat inflated walls. The possibility of an attempt on the part of the captive to escape by the place where the margins of the lamina meet is met by the circumstance that the edges of the incurved margins are furnished with sharp indentations turned towards the interior of the cavity enclosed between the lobes (see fig. 28<sup>5</sup>).

Amongst the prisoners we find the same company as in the traps of *Utricularia*, namely, small species of *Cyclops*, *Daphnia*, and *Cypris*, larvae of aquatic insects, and not infrequently also species of *Navicula* and other free and solitary Diatomaceæ.

How the prey is killed and digested has not yet been ascertained. It does not in any case take place so quickly as in *Dionaea*, for instances have been seen of animals still living in their prison six days after being caught. But, at last, movements and vital actions cease, and if after a couple of weeks the two lobes of the lamina are pulled apart, the only contents to be found are shells, bristles, rings, and siliceous skeletons, whilst everything soluble has vanished, having evidently been absorbed.

Very similar to the species distributed through Southern and Central Europe are *Aldrovandia australis*, a native of Australia, and *Aldrovandia verticillata*, inhabiting tropical India. The fact that the remains of small aquatic beetles and other creatures have been found within their closed laminæ, leads us to the conclusion that they act as entrappers of animals in the same way as *Aldrovandia vesiculosa*.

#### CARNIVOROUS PLANTS WITH ADHESIVE APPARATUS.

The forms constituting the third section of carnivorous plants neither have pitfalls nor move in response to the contact of animal matter, but the leaves act as motionless lime-twigs, their glands having the power of pouring out sticky substances to capture prey, and juices to digest it, being able besides to re-absorb the albuminoid compounds dissolved. The most striking representative of this section,

and the one most accurately studied, is the Fly-catcher (*Drosophyllum lusitanicum*), which is indigenous to Portugal and Morocco, and is shown in the illustration on p. 155. This plant differs from all the carnivorous kinds hitherto discussed in respect of habitat, inasmuch as it does not grow under water or even in swampy places but on sandy ground and dry rocky mountains. The stem in robust specimens is nearly 9 inches high, and bears, on a few short branches at the top, flowers from 2 to 3 cm. in diameter. The leaves are very numerous and particularly crowded round the base of the stem. Their shape is linear and much attenuated towards the filiform tip, whilst the upper surface is somewhat hollowed so as to form a groove. With the exception of these grooves, the leaves are entirely covered with beads, which glisten in the sunshine like dewdrops; and it is to this circumstance that the plant owes its name of *Drosophyllum*, i.e. Dew-leaf. The glittering drops are the secretion of glands, which in form remind one in some respects of the long-stalked glands of the butterwort, and in others of those of the Sun-dew (*Drosera*). They resemble the latter in their red coloration, in the fact that the pedicel bearing the gland contains vessels whilst the glands themselves have oblong cells with internal walls thickened by fine spiral ridges, and further, in the circumstance that the secretion covers the gland with a colourless film in the form of a drop. But in shape they especially resemble the glands of the butterwort, being just like little mushrooms.

Besides these glands, which are borne on stalks of unequal lengths and are plainly to be distinguished with the naked eye, there are also very small sessile glands. These latter are colourless, and in particular differ from the stalked variety in the fact that they discharge an acid liquid only when they come into contact with nitrogenous animal matter, whereas the secretion in drops on the stalked glands is secreted without any such contact. This secretion is acid and extremely viscid. It has the property of adhering immediately to foreign bodies coming into contact with it, though it is readily withdrawn from the gland itself. When an insect alights on the leaf, its legs, abdomen, and wings instantly stick to the drop touched by them. The insect, however, is not held fast by the gland which secreted that drop, but, being able to move, drags the drop off the gland. Its movements bring it into contact with other drops, which thereupon are similarly detached from the glands; and so, in a very short time, the insect is smeared with the secretion from a number of glands. Thus clogged and overwhelmed, it is no longer able to crawl along, but, suffocating, sinks down to the sessile glands which cover the surface of the leaf at a lower level. All the soluble parts of its body are then dissolved by means of the secretion of these glands and are afterwards absorbed.

The glands replace the drops of secretion of which they are despoiled with great rapidity. The quantity of acid liquid secreted is, in general, very great, so that it is not surprising to find *Drosophyllum* covered at the same time with remains of besmeared dead bodies drained of their juices, and with still struggling insects which have recently alighted and become clogged. The number of animals caught by the leaves of a single plant is very great; and even people who are not

otherwise interested in the vegetable world are impressed by the sight of a plant with its leaves covered with a number of insects adhering to them as though they were lime-twigs. In the neighbourhood of Oporto, where *Drosophyllum* grows abundantly, the peasants use these plants instead of lime-twigs, hanging them up



Fig. 30.—The Fly-catcher (*Drosophyllum lusitanicum*).

in their rooms, and so getting rid of numbers of troublesome flies which stick to them and are killed.

A number of other plants have the power, though in a less conspicuous degree than *Drosophyllum*, of obtaining additional nitrogenous food out of adherent animals by means of secretory and absorptive glands. Such are many species of primulas, saxifrages, and house-leeks, which bury their roots in cracks and crevices of rock (e.g. *Primula viscosa*, *P. villosa*, *P. hirsuta*, *Saxifraga luteo-viridis*, *S. bulbifera*, *S. tridactylites*, *Sempervivum montanum*), secondly, caryophyllaceous

plants and species of the caper order (e.g. *Saponaria viscosa*, *Silene viscosa*, *Cleome ornithopodioides*, *Bonchea cohiteoides*), and lastly, a series of plants which flourish in peat-bogs and upon deep beds of humus, such as *Sedum villosum*, *Roridula dentata*, *Byblis gigantea*, and many others besides.

It would, however, be erroneous to suppose that in all cases where a sticky coating occurs on leaves and stem a solution and digestion of the insects adhering to the viscid parts is necessarily denoted. In many instances structures of this kind, which are analogous to lime-twigs, are a means of protecting honey-bearing flowers against unwelcome guests belonging to the world of insects, as will be explained in greater detail later on. Glands secreting a viscid substance may, no doubt, often possess two kinds of function—they may, on the one hand, prevent unbidden animals from approaching the honey, and, on the other, turn to advantage such insects as are tempted by immoderate craving to step upon the perilous path leading to the honey-receptacles and so adhere to it and die, by dissolving their flesh and blood with the aid of the secretion and then absorbing them.

Many plants have, on the epidermis of their leaves, structures corresponding in form to the glands of insectivorous plants, but which do not discharge secretions either spontaneously or when irritated. On the other hand, these structures have the power of imbibing water, and are, in this relation, of the greatest importance to the plants in question. Although the more detailed treatment of them is postponed until we have occasion to deal with the absorption of water by aerial organs, it is advisable to refer now to the fact that chemically pure water only very rarely reaches the interior of a plant by means of the absorptive organs mentioned. Sulphuric acid is almost always introduced with atmospheric water, and in some circumstances ammonia also. However trivial the amount of the nitrogen conveyed to plants in this way, it must not be undervalued, at all events in the case of those which are only able to acquire small quantities of nitrogenous compounds from the ground by means of their roots. Now, it is very probable that plants of this kind do not reject even other nitrogenous compounds which are brought with the water from the atmosphere to their aerial leaves. The foliage-leaves of many plants display contrivances whereby rain-water is often retained for a considerable time in special hollows. In these depressions there is invariably a collection of dust-particles, small dead animals, pollen-grains, &c., which have been blown in by the wind, whilst rain trickling down the stem brings very various objects with it from higher up and washes them into these reservoirs in the leaves. Sometimes too a few animals are drowned in the water-receptacles. As a matter of fact, the water in the hollows of the leaves of the Peltate Saxifrage and of Bromeliaceæ, in the inflated vaginæ of many umbelliferous plants, and in the cups formed by the coalescence of opposite leaves in many Gentianæ, Compositæ, and Dipsacæ, is always brown-coloured, and contains nitrogenous compounds in solution, derived from the decaying bodies of dead animals which have fallen into these receptacles.

If absorbent organs are present in the reservoirs in question, the water, together

with the nitrogenous compounds dissolved therein, is absorbed without delay. Hollows of this kind occurring in foliage-leaves only differ from those above described as developed on sarracenias in being destitute of special contrivances for decoying animals into the traps, and for rendering their escape from the latter impossible. It cannot be denied that through forms of this kind a gradual transition has been proved to exist between plants which absorb nearly pure water by means of their foliage-leaves and those which capture animals. And, further, amongst the latter we find all gradations of mechanism from *Drosophyllum* and the *Primulas* with their epiphyllous secretory glands up to the Fly-trap (*Dionaea*), which exhibits the most complex apparatus of all for capturing and digesting prey, and in which division of labour is carried to its highest development by the communities of cells constituting the foliage-leaves.

It is not surprising that the first apparatus for capturing and digesting insects to be noticed, to have its functions recognized and to be described, was that of *Dionaea*. But it strikes one as all the more strange that of late the question has repeatedly been mooted in the very case of *Dionaea*, as to whether the capture and digestion of insects is not injurious instead of beneficial to these plants. Gardeners, who have cultivated *Dionaea* in greenhouses, have made the observation that individuals protected from the visits of insects thrived at least as well as those whose leaves were covered with bits of meat, &c., or, to employ the usual phrase, were fed with meat. It has also been found that a leaf cannot stand more than three meals; indeed, it often happens that even after the first occasion of digesting a bit of meat, the leaf concerned shows signs of having been injured by the repast. That is to say, a long time elapses before leaves which have digested a largish albuminoid mass regain their normal irritability; and often they wither and die. If cheese is placed on *Dionaea*, it is true the leaf closes over it, and there is a commencement of the process of solution, but before the latter is accomplished the leaf turns brown and perishes. Yet if *Dionaea* were obliged to lose a leaf after every meal, the result would be very disadvantageous.

As against these considerations, we have first of all to remark that the absorption of nutriment takes place in nature in a manner differing materially from the phenomenon in greenhouses. A leaf of *Dionaea* in the wild state is protected against the possibility of receiving too plentiful a dose of albuminoid substances at a time. Insects so large as not to allow the lobes to close together over them slip out again, and only small ones are caught and retained. When, in the latter case, one deducts the chitinous coat, and in general all parts not susceptible of being digested, such a small quantity of albuminoid compounds is left that, compared with it, the little cubes of meat used in the experiments made in greenhouses must be looked upon as an exceedingly sumptuous repast. But that so small an amount of nitrogenous food as is to be derived from a tiny captured insect does not act injuriously, follows from the fact that dionæas growing wild flourish excellently, and do not exhibit the brown discoloration of the leaves which is caused in a greenhouse by placing bits of cheese upon them. If the absorption of nitrogenous

aliment from prey were injurious to *Dionaea*, the plant would certainly have died out long ago. If, therefore, cultivated specimens of *Dionaea* have suffered from being fed with meat, fibrin, cheese, and other such materials, only this much is proved, that the nutriment in question was not beneficial to them owing to its quality or to its being too concentrated.

As regards the other point, that *Dionaea* thrives well under cultivation, even when all visits from insects are excluded, we must, on the other hand, bear in mind that the successful growth of *Dionaea*, like that of *Drosera*, *Pinguicula*, &c., is not conceivable unless in some way or another the nitrogen indispensable for the construction of the protoplasm is conveyed to the individuals in question. The source from which it is taken varies according to the site. If the roots are buried in deep sods of bog-moss upon a flat expanse of moorland, the supply of nitrogen from the ground, and also from the air, will be extremely limited, and probably insufficient, and, in the latter case, the nutriment derived from the dead bodies of captured insects would be not only useful and beneficial, but may be even essential. If, on the contrary, the place where the plants have been reared or have grown up spontaneously is such that they can obtain the requisite nitrogen from the ground or air, they are able without harm to dispense with the available source of nitrogen afforded by the capture of insects. It is worthy of notice that insectivorous plants always grow wild only in places that are poorly supplied with nitrogenous food. The majority occur in pools fed by subterranean water, whose course lies through layers of peat, or in the spongy peat itself, or in the sods of *Sphagnum*. Others are rooted in deep chinks in the stone on the declivities of rocky mountains, whilst yet others occur in the sand of steppes. The water available in such situations for absorption by the suction-cells is, to say the least, very poorly furnished with nitrogenous compounds; and the quantity of these compounds passing from the ground into the air at the places mentioned is extremely minute and inconstant. Under these circumstances, the acquirement of nitrogen from the albuminoid compounds of dead animals is certainly of benefit, and all the various pitfalls, traps, and lime-twigs are explained as contrivances by means of which this advantage is secured.

---

#### 4. ABSORPTION OF NUTRIMENT BY PARASITIC PLANTS.

Classification of parasites.—Bacteria.—Fungi.—Twining parasites.—Green-leaved parasites.—Toothwort.—Broom-rapes, *Balanophoræ* and *Rafflesiacæ*.—Mistletoe and *Loranthus*.—Grafting and budding.

#### CLASSIFICATION OF PARASITES.

The ancients understood by parasites people who intruded uninvited into the houses of the rich in order to obtain a free meal. The designation was first applied to plants by an eighteenth century botanist, named Micheli, in his work "De Orobanche" (1720) wherein are described amongst others, many kinds of "plantæ secundariaæ aut parasiticæ". Micheli included under the term plants which withdraw organic compounds from living plants or animals, thus sparing themselves the labour of forming those compounds out of water, salts, and constituents of the air. For a long time all epiphytes, including mosses and lichens growing on the bark of trees, and indeed even many climbing plants, were held to be parasites. Thus, it is not long ago that *Clusia rosea*, which occurs in the Antilles, was described as a regular vampire, in whose embraces other plants met their death; and it has been asserted respecting a whole series of other plants of the tropical zone, including, for instance, several species of fig, that they attach their stems and branches to other trees, divest themselves of their bark, and cause the death of that of the neighbour attacked as a consequence of the pressure which they exert. The young wood of the invader would then come into direct connection with the young wood of the plant assailed, and the possibility would thus be afforded of draining the latter of all its juices.

These assumptions, at least as regards the exhaustion of juices, have not been confirmed. When individuals of species of *Clusia* or *Ficus*, which have roots buried in the earth, and are themselves already grown up into stately leaf-bearing plants, attach their flattened stems and branches to other plants, investing them so completely as to interfere with the process of respiration; this constitutes, at all events, an invasion of one of the most important of the vital functions of the plant attacked, and may ultimately cause its death; but the killing is not under these circumstances due to drainage of juices, but is brought about by suffocation. Lichens, too, when they cover the bark of trees with a close-fitting mantle, may possibly restrict the process of respiration through particular parts of the cortex, and thereby injure the development of the tree in question; but they are not on that account to be looked upon as parasites any more than the fructifications of the species of *Telephora*, and other Basidiomycetes, which grow up rapidly from the ground, and, spreading out like plastic doughy masses, envelop all objects which come in their way, and ultimately stifle such as are living, namely, grass haulms, bilberry bushes, &c. Even creepers, which impose woody stems upon the trunks of young trees, winding round them like serpents, and restricting their circumferential growth at the parts in contact with the coils, so that ultimately the latter lie

imbedded in regular grooves in the cortex, ought not to be considered as parasites. The *Lonicera ciliosa* of North America, represented in fig. 31, may be taken as an example of creepers of this kind. They only interfere with the conduction of the constructive materials generated in the green foliage, preventing, in particular, the



Fig. 31.—*Lonicera ciliosa* in South Carolina.

part of the axis below the strangulating coils from being supplied with those materials; and so at last they cause the whole trunk, which serves as their support, to dry up. The assertion may then be made that the young tree assailed has been strangled or throttled by the creeper, but not that the latter has drained it of juices and adapted them to its own use. Still less would the statement be applicable to the numerous brown and red sea-weeds, which settle upon the ramifications of the great species of *Sargassum*, or of the innumerable Diatomaceæ, which often entirely

cover both fresh and salt-water plants. In still inlets of the sea it is not rare to see the larger sea-wracks with smaller specimens clinging to them, whilst Florideæ are fastened to the latter, and minute siliceous-coated diatoms to the Florideæ. Even in fresh water, e.g. in cold and rapid mountain streams, we find little tufts of *Chantransia* or *Batrachospermum* developed as epiphytes upon the black-green filaments of *Lemanea*, and on the former, again, Diatomaceæ. One of these Diatomaceæ, which, from its resemblance to a scale insect, has received the name of *Cocconeis Pediculus*, is especially conspicuous, and is often found by the score upon the green filaments of Algae. Such a connection does, no doubt, suggest the idea that the *Cocconeis* drains the green algal cells of nutriment; nevertheless, such an assumption is not well founded, and if algae, beset by *Cocconeis*, derive injury at all from their presence, it is chiefly owing to a restriction of their absorption of nutrient substances from the surrounding water and to interference with their respiration.

The distinctive property of true parasites does not lie, therefore, in the habit of growing upon other plants and animals, or even in the fact of killing their living supports, but resides exclusively in the withdrawal of nutrient substances from the living vegetable or animal bodies which they invade.

The plants and animals attacked and drained of their juices by parasites are called hosts.

From the point of view of food absorption, true parasites may be classified in three groups. The first group includes generally all microscopic forms which live in the interior of human beings and animals, chiefly in the blood; the second comprehends fungi possessing mycelia, which have the power of withdrawing by the entire surface of their filamentous cells, or by clavate outgrowths of the same, nutritive material from the tissues of the host invaded by them; and the third group comprises flowering plants wherein the seedling, upon emerging from the seed, penetrates into the host, by means of suction-roots or some other part which subserves the function of a suction-root, so as to absorb juices from the host.

#### BACTERIA. FUNGI

In treating of parasites of the first group, we must, in the first place, refer to several of the unwelcome visitors known by the name of Bacteria. They appear to be invariably unicellular, sometimes spherical, sometimes shortly cylindrical or rod-shaped; some are straight, and others curved in arcs or spirals; a few are non-motile, whilst some are actively motile. The largest forms have a diameter of  $\frac{1}{500}$  mm.; the smallest do not measure more than  $\frac{1}{5000}$  mm., and are reckoned amongst the minutest organisms hitherto revealed by the aid of the best microscopes. In liquids of suitable chemical composition and temperature, they multiply with extraordinary rapidity, reproduction being effected by division. The rod-shaped cells elongate somewhat and divide into two equal halves, each half, when grown to a certain size, divides once more into two, and so on without limit.

The process gives the impression of being a repeated splitting of the cells, and this is the origin of the name of Fission-fungi (Schizomycetes) used to designate these organisms. It has been observed that within 20 minutes a bacterium-cell grows enough to be able to divide or split into two, and hence it has been calculated that from a single cell, under favourable external conditions, upwards of 16 millions of similar cells are produced in 8 hours; and in 24 hours many millions of millions.

It is this very capacity for rapid multiplication that gives so great an importance to Bacteria as parasites. For multiplication can only take place at the expense of the juices and nutrient substratum in which they live. If this nutrient substratum is to afford materials for constructing the millions of millions of cells produced within two periods of 24 hours, a far-reaching transformation is inevitable. Now, for certain bacteria, the blood, with its albuminoid compounds and carbohydrates, is an extremely favourable medium of nutrition; moreover, the temperature of the blood of men and other mammals ( $35^{\circ}$ - $37^{\circ}$ C.) could not be more suitable for the development of bacteria. Hence, it is readily intelligible that if a single parasitic bacterium-cell gets into the blood, it may be the origin of innumerable other cells, and that these are in a position, in a comparatively short time, to alter and decompose the whole mass of the blood. Owing to their extraordinary minuteness, bacteria are able to penetrate from outside into the channels of the blood by a number of spots: every abrasion, pin-prick, and sore place, may become an entrance-door: so, too, through all the external orifices of the various canals in the bodies of men and animals, the bacteria can enter, especially through the passages to the respiratory organs—and it becomes more and more probable that bacteria, diffused in the air, are in the main introduced into the respiratory organs by the process of breathing, thence penetrating into the finest blood-vessels, the so-called capillaries, and so pass into the current of the blood.

As regards the parasitic action of bacteria when they have penetrated into the bodies of men and animals, the supposition is that the protoplasm of each bacterium works as a ferment upon the environment, splitting up the chemical compounds in immediate proximity to it, and attracting and incorporating such products of the decomposition as are necessary for its own growth. Parasites with this method of operation act, at all events, much more destructively than those which, although they too absorb part of the host's juices, yet do not enter upon the necessary decompositions until the juices have passed into the cavities of their own bodies, and, therefore, do not alter the constitution of the unabsorbed residue. When the component parts of the blood are split up and resolved by bacteria, the nutrition of the host must be especially disturbed, and so must all the functions of the organs through which the blood perpetually circulates. Ultimately it may culminate in the organs ceasing to exercise their functions, and in the death of the host. When one remembers how fast the blood is pumped by the heart's action into every part of the body, it becomes intelligible how bacteria, possessing the power of decomposing the blood, may also cause the death of the host at very short notice, as we have occasion to observe whenever there is an epidemic of cholera.

That numerous diseases affecting men and animals are caused by bacteria is established beyond question. Indeed, the conviction is gradually gaining ground that all infectious illnesses are occasioned by bacteria, and that the contagious matter which used to be called virus or miasma, but as to the nature of which people formerly had only very confused notions, consists of parasitic bacteria. Different phenomena in organisms in which illness has been induced by infection point to differences in the decompositions effected by the bacteria. But a particular kind of parasitic cell can only set up the same decomposition in any given liquid. If, therefore, the products of separation or decomposition vary in one and the same liquid, this can only be attributed to a difference in the impetus causing decomposition, and therefore to a difference in the parasitic cells; in other words, we are justified in assuming that every distinct infectious disease is due to a special kind of parasitic bacterium. This assumption is believed to be warranted even when no difference in the form of the bacteria is to be discovered which is discernible to sight or demonstrable by the expedients of research.

Most of the parasitic bacteria regarded as causes of diseases in man and beast are moreover capable of being very clearly distinguished from one another by the shape of their cells. The bacterium supposed to be the cause of diphtheria (*Micrococcus diphthericus*) presents itself in the form of minute spherical cells crowded together in close masses. The bacterium which causes anthrax in cattle (*Bacterium Anthracis*) has straight rod-like stationary cells. In the blood of people suffering from relapsing typhus, infinitesimally fine spiral filaments (*Spirochaete Obermeieri*) are found during the fever, whilst in the intestines of cholera patients, the comma-bacilli, so frequently described, occur; and in these cases, likewise, the organisms are brought into causal connection with the illnesses mentioned respectively. The answer to the question as to whether parasitic bacteria are developed and propagated in dead bodies also, thus becoming saprophytic, and, in general, the detailed description of the organisms, which are so important a factor for the weal or woe of humanity, are reserved for another section.

The second group of parasitic plants, according to the classification above given, includes several thousands of different kinds of moulds, toad-stools, and Discomycetes, which, notwithstanding great diversity in the conditions of life, dissimilarity in the history of their development, and endless variety in the form of their fructifications, yet exhibit great uniformity in respect of food-absorption and in their methods of attacking and draining their hosts. Spores, conveyed by currents of air or carried by animals, germinate under the influence of atmospheric moisture wherever they happen to come to rest. Tubular thin-walled cells, called hyphae, emerge from them and endeavour to grow into the stems, branches, leaves, or fruits of the host, sometimes horizontally, sometimes from above downward, sometimes up in the opposite direction. Many select spots where the resistance offered is nil or only very weak: they grope about on the surface of the host until they find a stoma, and then use it as an entrance, and so pass into the passages and lacunæ, of which the stomata are the orifices. Others seek out places where the

surface of the plant serving as host has become broken—wounds occasioned by animals, violent wind, hailstones, or the weight of superincumbent snow—and use these as means of ingress. Yet others adopt the shortest route by breaking through the wall and so effecting an entrance for themselves. The tips of the hyphæ and also of the outgrowths developed by them have the power of decomposing and destroying the membrane of cells in the living plant serving as their host. At the spots to which they apply themselves, little gaps are shortly produced in the cell-membranes, and through them the hyphæ penetrate, either in their entirety or by means of special processes, into the interior of the cells attacked. In this operation it does not matter whether the hypha concerned has just emerged from a germinating spore or is a ramification of a mycelium several years old, which has been quiescent for a time and then begun to germinate again vigorously; the power of perforating cell-walls is a property possessed by the one as much as the other.

The aspect of the host's epidermal cells at the places where the hypha comes into contact with its victim is, on the other hand, not quite such a matter of indifference. For plants liable to become hosts are not without contrivances for protecting themselves against intruders. Thus their epidermal cells have their external walls greatly thickened and invested with cuticle. Although the main object of this is merely to afford protection against excessive transpiration and desiccation of cells filled with sap, a thickening of the kind constitutes also a coat of armour which is not liable to be broken through by every hypha. Still greater security is afforded by a double or triple layer of thick-walled cells destitute of sap, such as a solid corky bark. Coats of this kind are not penetrated even by the most vigorous hyphæ. In order to gain admittance notwithstanding, many force their conical tips into the fissures and crannies of the bark, push the peeling scales apart or even burst them, and so succeed ultimately in reaching parts which are susceptible of being pierced and allow the hyphæ to conduct their mining operations with effect. In the majority of cases the parasite is not content with perforating and exhausting the superficial cells alone of the host; its hyphæ grow faster as they penetrate deeper, a process generally accomplished irrespective of the number or direction of the partition walls in their way. Thus the hyphæ of *Polyporæ*, which are parasitic in the wood of living trees, penetrate whole series of cells, now growing through a bordered-pit, now piercing the uniformly thickened part of the wall of a wood-cell (see fig. 32<sup>3</sup>). Others, as, for instance, the *Peronosporæ*, prefer to bury themselves in the passages between individual cells, i.e. in the so-called intercellular spaces. The hyphæ imbedded in this way then develop lateral outgrowths which perforate the walls of the cells adjoining the intercellular space, and upon entering the interior of the cells swell up to the shape of a club (see fig. 32<sup>1</sup>). By means of these clavate or almost spherical excrescences, which are named haustoria, the parasite sucks the substances required for its own nourishment from the living substance of the penetrated cells.

The hyphæ of the above-mentioned parasitic fungi have the peculiarity that in

proportion as the one end elongates the other dies away. Hence the same effect is produced as if the progressive motion of these hyphæ were like that of ship-worms. This impression is particularly strong in cases wherein one part of the mass of wood attacked exhibits hyphæ occupied with their mining operations and growing through partition walls, whilst the other part has been the scene of past activity, and exhibits numbers of drilled holes, but no longer any trace of hyphæ. The fact that a plant is thus invaded internally by the parasitic mycelia of fungi is not always betrayed by its external appearance. Sometimes the hosts remain somewhat backward in development, but this circumstance might be just as well due to other causes, perhaps to unsuitability of situation. It is not till the mycelia need once

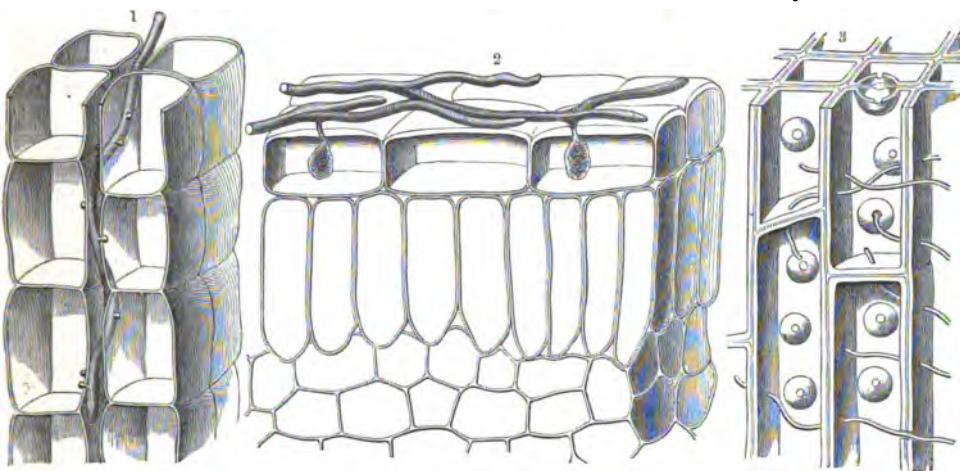


Fig. 32.—Hyphæ of Parasitic Fungi.

<sup>1</sup> Of one of the Peronosporæ. <sup>2</sup> Of a Mildew. <sup>3</sup> Of one of the Polypores.

more to multiply and distribute their kind that they emerge partially from the host; they then lift their spore-forming hyphæ above the surface, leaving it to the wind to distribute the spores as they are detached.

This process vividly recalls the similar behaviour of those water-plants which, in a similar manner, vegetate submerged for months, and only come to the surface at the flowering and fruiting seasons, in order to expose their flowers to insects, and their seeds to the breeze. We are also reminded of the saprophytic orchids already described, which nourish themselves and grow for years imbedded in the humus of woods, and then seize the opportunity afforded by a favourable summer to raise up in a few weeks flowering stems above the bed of the forest. As a rule the spore-bearing hyphæ, emerging from the hosts of parasitic fungi, are highly conspicuous both in form and colour. As well-known instances we may here mention the powdery, rust-coloured, chocolate-brown, or coal-black masses of spores, known by the names of rust and smut; the mealy, orange-coloured masses which make their appearance on the green stems and fruits of roses (*Æcidium* stage of *Phragmidium subcorticatum*), and the discomycetous *Peziza Willkommii*, which is parasitic in the branches of green larches, and exposes its fructifications beyond

the bark in the form of small scarlet shields. Again, we have the yellow *Polyporus sulfureus* with its immense yolk-coloured, bracket-like fructifications, which in the space of a week grow out from the trunks of larches, although the outward appearance of the host gives no indication of its being completely occupied internally by a mycelium. *Polyporus betulinus* and *P. fomentarius* likewise grow to a considerable size, and in both cases it is specially deserving of notice that the colour and structure of the surface of the fructification is surprisingly like the bark of the trees upon which they are respectively parasitic; that is to say, the fructification of *Polyporus betulinus* strongly resembles the whitish bark of the birch, and that of *Polyporus fomentarius*, parasitic on old beech-trees, exhibits the same pale gray as does the trunk of a beech.

Mildews form in some respects a contrast to these parasites whose hyphae penetrate into the interior of their hosts. They attack tender green leaves, stems, and young fruits, and accomplish their entire development upon the epidermal cells of the hosts. At first sight the parts assailed appear to be strewn with flour or dust from the road. But on closer inspection a delicate weft is to be distinguished, composed of filaments ramifying extensively upon the green substratum intersecting one another, uniting to form reticula, and in parts a regular felt-work covered at certain spots with the small dark spheres of the sporocarps. Individual hyphae of this weft adhere closely to the epidermal cells of the host, dissolve the outer walls of these cells at the points of contact, so as to make little apertures, and then develop processes which grow into the interior of the epidermal cells in question, assume a club-like form, and exhaust the cell-contents. The mycelia of mildews do not penetrate into the host beyond the epidermal cells. Fig. 32<sup>2</sup> shows a piece of a leaf of *Acanthus mollis* attacked by mildew, with hyphal suckers penetrating into the epidermal cells of the leaf. One of the best-known mildew fungi is the Vine-mildew (*Erysiphe Tuckeri*), which weaves itself over the epidermis of still green and unripe grapes, and has frequently manifested itself through the districts where the vine is cultivated in southern and central Europe in the form of a ravaging disease.

The protuberances sent by the hyphae, in the form of clavate swellings, or more rarely winding tubes, into the cells of the host-plants, correspond to the absorption-cells of land plants, and the conditions under which suction takes place are essentially analogous in the two cases. The absorption-cells on the roots of land plants do not take in all the substances in their nutrient substratum, and similarly the hyphae only appropriate by means of their organs of suction a portion of the contents of the cells invaded. They begin by dissolving and breaking up for this purpose the substances in the infested cells of the host. What compounds they then select from among the products of decomposition, and what they leave behind, cannot certainly be specified in detail. It is believed that, in many cases, tannin is appropriated first of all by parasites. The wood of a healthy oak, for instance, has a characteristic smell due to the abundance of tannin it contains, whereas the odour is not emitted by wood attacked by the mycelia of fungi, and this decayed

wood is destitute of tannin. It is natural to suppose, therefore, that the mycelium takes away and uses up the tannin. It has also been observed that wherever the hyphæ of the Pine-blister (*Peridermium Pini*) ensconce themselves, the nitrogenous parts of the protoplasm and the starch vanish, whilst turpentine remains behind, clinging in drops to the inner walls of the cells. These are, to be sure, very sparse data; but they show that the entire cell-contents are not absorbed by the parasite unaltered, or used in that condition as material for the building up of its own body.

Not only the contents of the cells preyed upon, but the walls as well, are partially used as food by the hyphæ which penetrate into the woody axes of arborescent angiosperms and gymnosperms. The mycelium of several species of *Polyporus* and *Trametes* begins by bringing the lignin in the cell-walls into solution, leaving nothing but a pale-coloured cellulose wall. Soon afterwards, the so-called middle lamella, which connects adjoining wood-cells, is also dissolved, and the colourless wood-cells, now almost like asbestos-fibres in appearance, fall apart at the slightest touch. When the wood of a larch has been infested by the mycelium of *Polyporus sulfureus*, there are always deep furrows running obliquely on the internal walls of the wood-cells; this loss of substance, too, can only arise from the solution, and absorption as nutriment, of parts of the walls by the action of the hyphæ.

All decompositions and alterations of structure of the above kind within the precincts of the host's cells are naturally followed by a disturbance of function, and ultimately by death. The entire plant is, however, but rarely killed by parasites belonging to this group. The decomposition by bacteria of a mammal's blood, though at first confined to a particular part of the body, spreads in a moment throughout the whole organism, owing to the heart's action and the circulation of the blood. But the decomposition taking place in the manner just described, through the intervention of hyphæ, propagates itself, on the contrary, only very gradually from the cells immediately attacked to their neighbours, and it gets weaker and weaker as the distance from the site of the invasion increases, a circumstance to which we shall recur later on when discussing the phenomena of fermentation and decay. The nature of the parasite and the power of resistance of the host have undoubtedly influence on the rate of distribution. In many cases alteration is limited to the cells attacked and those immediately adjoining, so that the area destroyed is circumscribed. It is manifested on fresh, green leaves, often merely in the form of small, isolated, yellow, brown, or black spots and patches, which only slightly interfere with the activity of the leaf, and do not cause it to change colour, wither, or fall off any earlier. In other instances, however, the entire leaves and stem do undoubtedly become flaccid and shrivelled and dried up into a black mass, looking as though they had been carbonized; or else corruption, such as that which is excited by bacteria, invades the whole mass.

As above stated, when the wood in the trunks of trees is perforated and consumed by hyphæ it is resolved into fragments. It becomes rotten, takes the form of an asbestos-like, or crumbling and pulverulent mass, and is then obviously no longer capable of fulfilling its various functions in the living plant. If the

invasion is limited in extent, and the host succeeds in surrounding the area of infection with a rampart of cells capable of resistance, and not liable to be pierced by the hyphae, then the tree may live for years although its trunk is infested, and in parts rotten. Such is also the case when particular branches of a tree are alone attacked by the mycelium of a fungus. When, for example, the branch of a larch is assailed by the mycelium of the Discomycete, *Periza Willkommii*, the fact is first manifested externally by the fascicles of needles on the branch in question becoming discoloured in the summer, and acquiring, prematurely, an autumnal appearance; so that, among the fresh green shoots, individual branches are to be seen bearing golden-yellow needles. Towards autumn, scarlet cup-shaped fructifications make their appearance upon the surface of the bark on the branch; in the course of the next few years the whole branch as a rule dries up, withers, and dies. It is then broken by the first violent shock of wind and falls to the ground; but the tree, disengaged of the dead bough, continues to grow unharmed, and to put forth green shoots. It is only when almost all the branches of the larch are infested by the mycelium of this fungus that the whole tree perishes as a result of the invasion.

Certain groups of plants are specially liable to be attacked by parasitic fungi, and there are some conifers and angiospermous trees in which the same stem is colonized by three, four, or five kinds of parasite. The green foliage leaves of large numbers of flowering plants are also apt to be selected by parasites, as also are their roots, tubers, and bulbous structures. Many parasites only attack the anthers in flowers; others, as for instance the ergot, only the young ovaries. Parasitic fungi are rarely found on mosses or ferns; whereas a considerable number of parasites settle upon lichens and even on the fructifications of fungi, even moulds being infested by other fungi; for example, a fungus named *Piptocephalis Freseniana* is parasitic upon the very common mould, *Mucor Mucedo*.

A fungus known by the name of *Cordiceps militaris* is parasitic in the caterpillars and pupæ of butterflies and other insects, and its relatively very large fructification at length bursts out of the body infested by the mycelium in the form of a club nearly 6 cm. long. This clavate structure, built up at the expense of the insect's flesh and blood, produces tubular cells in special receptacles, and, inside these, little rod-like spores, which afterwards fall out and infect other caterpillars, developing within the bodies of these animals into a hoary mycelium and ultimately causing their death. The disease of silk-worms, known as muscardine, is likewise occasioned by a species of *Cordiceps*. We must also refer here to the widely-distributed *Empusa Muscae*, a mould which attacks flies and causes every autumn a regular epidemic amongst house-flies. The flies so often seen at that season adhering stiff and dead to window-panes are surrounded by a whitish halo, and this is composed of a conglomerate of spores thrown off by the mould which is parasitic upon the flies and causes their death. Parasitic fungi have also been observed in the human skin, and recognized as the causes of skin-diseases. For instance, to the mould *Achorion Schoenleinii* is due the disease of the skin popularly known as

"honey-combed ringworm", and named *Favus* by doctors; dandruff (*Pityriasis versicolor*) is produced by *Microsporon furfur*, and *Herpes tonsurans* by *Trichophyton tonsurans*. The latter has a remarkable effect on the hair, causing it to fall out and leave the part of the skin affected bald.

Water-plants are attacked by parasitic fungi comparatively rarely, which is the more noteworthy because such large numbers of non-parasitic epiphytes settle upon the filaments of green algae, and on the brown Fucoidæ, and red Florideæ. Minute

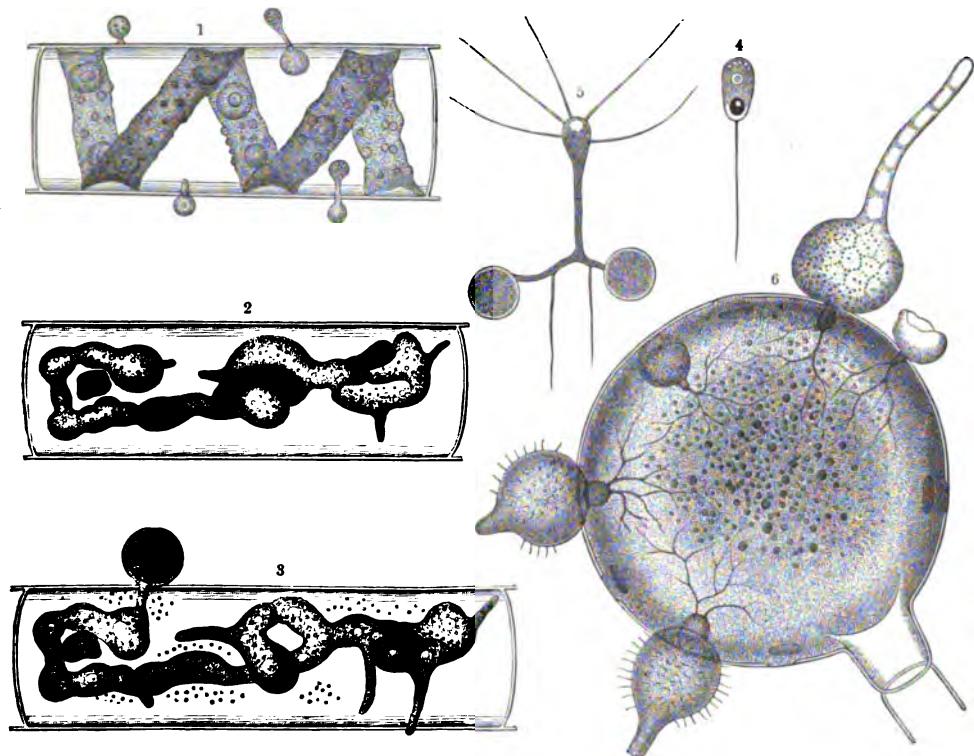


Fig. 33—Parasites on Hydrophytes.

1, 2, and 3 *Lagenidium Rabenhorstii*. 4, 5 *Polyphagus Euglena*. 6 *Rhizidiomyces apophysatus*.

forms of fungi, invisible to the naked eye, and belonging to the Chytridæ and Saprolegniæ, are parasitic upon green algal filaments, especially on the fresh-water species of the genera *Edogonium*, *Spirogyra*, and *Mesocarpus*. One of these microscopic parasites is represented in fig. 33<sup>1, 2, 3</sup>, and bears the name *Lagenidium Rabenhorstii*. It develops non-ciliated, spherical swarm-spores, which lay themselves upon the walls of *Spirogyra*-cells, perforate them, and insert a club-like process. The protuberance forthwith becomes a tube, which increases rapidly in size in the interior of the cell, ramifying and completely destroying the bands of chlorophyll. The branched tubes of *Lagenidium* reproduce themselves in two ways at the expense of the host's cells infested by them: they form on the one hand so-called oospores by means of fertilization, and on the other sporangia. The latter process is clearly shown in fig. 33<sup>1, 2, 3</sup>. In this case, one of the tubular

processes of the parasite fungus pushes out of the cell-cavity of the invaded *Spirogyra* into the surrounding water again and there swells up into a spherical vesicle, within which the protoplasm divides into eight spores. These spores are then set free as swarm-spores and attack new healthy *Spirogyra*-cells.

Materially different is the behaviour of the parasite *Chytridium Ola*, which attacks the green cells of fresh-water *Edogonieæ*. Its roundish swarm-spores are furnished each with one long cilium, and swim, searching about in the water until they meet with an *Edogonium*-cell to their taste just occupied in the formation of oospores. When they find one, they fasten upon it and send infinitesimally fine hair-like tubes (which have been called rhizoids) into the interior. By means of these tubes they derive their nutriment from the host. The body of the parasite, which remains outside the invaded cell, increases in size, and at length grows out into a sporangium; the latter opens at the top by a lid and once more sets free swarm-spores into the surrounding water.

*Polyphagus Euglenæ*, a member of the Chytridææ, is parasitic on the green cells of *Euglena* living in water. The swarm spores of this microscopic fungus (see fig. 33<sup>4</sup>) are oval and furnished, like those of *Chytridium Ola*, with a long cilium. They swim about the water with the non-ciliate extremity leading, so that the cilium appears to be a tail at the posterior end. As soon as these swarm-spores have come to rest, they assume a spherical form and send out in all directions thin, hair-like tubes, which search for a host. When a tube reaches an *Euglena*-cell, it penetrates into the body of the latter, drains it, and, continuing to grow, produces fresh hair-like tubes, which attack other green *Euglena*, often linking together dozens of them (see fig. 33<sup>5</sup>). In this way the *Polyphagus* grows apace and becomes a comparative large oblong vesicle, whilst the protoplasm within it divides into a number of parts. These, again, turn into swarm spores, with long ciliary filaments, and they slip out of the vesicle and may attack fresh *Euglena*.

Curiously enough, even saprophytic water-plants destitute of chlorophyll are sometimes attacked by parasites, and that, indeed, by species belonging to the same group. Thus, for instance, the species of *Achlya* growing on the dead bodies of fishes and other animals which have perished in the water, are themselves infested by small parasitic Saprolegniaceæ and Chytridææ. The example of these minute parasites represented in fig. 33<sup>6</sup> is named *Rhizidiomyces apophysatus*, and its host is *Achlya racemosa*. The swarming spores of the parasite lay themselves, in the manner described in previous instances, upon the spherical oogonia of *Achlya*, and insert extremely fine hair-like tubes into the interior of the cells attacked. These ramify like roots in the *Achlya*-cells, exhaust them of nutriment, grow perceptibly, and at length form spherical swellings, which, after reaching a certain size, break through the walls of the host-cells, project from the opening, and, lastly, push out in each case a sporangium. The latter produces a number of swarm-spores, which escape into the water and are able to seek fresh prey.

We cannot here enter into details respecting the other kinds of reproduction occurring in the minute fungi parasitic upon hydrophytes. This is the right place,

however, to mention the fact that the various species of Chytridææ and Saprolegniacæ do not content themselves with plants that are second-rate hosts, but exercise a selection amongst the different green algæ living in the water. It is astonishing to find that the swarm-spores invariably swim to cells whose protoplasm affords the most suitable nutrient basis for them, and attach themselves to those cells only, and never on other species unadapted to their requirements.

#### CLIMBING PARASITES. GREEN-LEAVED PARASITES. TOOTHWORT.

The third group into which parasites were divided at the beginning of this chapter is composed of flowering plants throughout. According to their method of attacking the host for the purpose of absorbing nutriment from it, they range themselves in six series. In the following pages we shall discuss the characteristics of each series as manifested in the most remarkable forms belonging to it.

The first series includes plants destitute of green leaves and of chlorophyll in general, whose seeds germinate on the ground and send forth each a filiform stem, which brings itself, by means of peculiar movements, into contact with the host-plant, coils round it, and develops organs of suction whereby it takes nutriment from the plant assailed.

To this series belong the genera *Cassytha* and *Cuscuta*. The former includes some thirty species, all of which appertain to warm climates. Most of the *Cassytha* inhabit Australia, where they attack, in particular, the copses of Casuarinæ and Melaleucæ, fastening their wart-shaped, or, in many cases, shield-like or discoid suckers upon the young green shoots of those plants. Several species also are indigenous to New Zealand, others to Borneo, Java, Ceylon, the Philippines, and the Moluccas. South Africa, too, is the home of a few *Cassytha*, and one species (*C. Americana*) is distributed over the West Indies, Mexico, and Brazil. A European, seeing these parasites with their twining, thread-like, leafless stems, and their flowers aggregated in capitula, umbels, or spikes, takes them at first to be species of the genus *Cuscuta*, popularly called Dodder. That these plants should be most nearly related to laurel-trees is the last thing one would expect. Examination of the flowers and fruit reveals, it is true, a close resemblance to those of laurel and cinnamon trees, and, therefore, these *Cassytha* are rightly placed by systematic botanists among the Lauraceæ. But in respect of food-absorption, as in general aspect, they are entirely analogous to the various species of the genus *Cuscuta*, which belong to the family of Bindweeds (Convolvulaceæ). The last-named genus is even more variously differentiated than the genus *Cassytha*, and includes about fifty species dispersed pretty evenly over the whole world. Every part of the world has its own characteristic forms. One group occurs in California, Carolina, Indiana, Missouri, and Mexico, another in the West Indies, Brazil, Peru, and Chili, a third at the Cape of Good Hope. Other species are natives of China, the East Indies, the steppes of Central Asia, Persia, Syria, the Caucasus, and Egypt.

A comparatively large number of species, i.e. twenty-five, are distributed through central and southern Europe. A few have been introduced recently for the first time with seeds from the New World, as, for instance, *C. corymbosa*, which was accidentally conveyed with lucerne seeds from South America to Belgium, and has latterly begun to range over central Europe.

The various species of *Cuscuta* attack chiefly small herbaceous, suffruticose, and shrubby plants; but a few American species coil themselves round branches growing at the top of the highest trees. Notice has been especially drawn to certain European species on account of their disastrous effects upon cultivated plants. The most famous is *Cuscuta Trifoliae*, known as the Clover-Dodder, the appearance of which in clover-fields causes so much anxiety to farmers, and which is so difficult to exterminate. Another unwelcome visitor is *Cuscuta Epilinum*, which coils round flax stems and hinders their growth, and a third species, *Cuscuta Europaea*, sometimes ravages hop-plantations. This last is, indeed, the most widely distributed of all the Cuscutas, and extends from England over central Europe and Asia to Japan, and southwards as far as Algiers. It is parasitic not only on hops, but also on elder, ash, and various other shrubs and herbs; in particular it exhibits a preference for nettles.

The seeds of this species, and of Dodders in general, germinate on damp earth, on wet foliage undergoing putrefaction, or on the weathered bark of old trunks. The seedling, which in the seed lies imbedded in a cellular mass full of reserve-food, is filiform and spirally coiled. It is twisted once, or once and a half, and is thickened at one end like a club. In true Cuscutas, no trace of cotyledons is to be perceived, nor does one find vessels in the interior of the seedling; but chains of cells arranged with great regularity are noticed in the axis of the filiform body, and are easily distinguished from the surrounding cells. In nature, the seeds, after falling to the ground and lying there through the winter, do not germinate till very late in the following year, i.e. at least a month later than the majority of the other seeds reaching the same ground simultaneously with them. Perennial herbs, also, have, by the time that germination takes place, already developed shoots from their subterranean roots or rhizomes above the surface of the ground, later a circumstance of great importance to the parasites. If a *Cuscuta* were to germinate early in the spring, it would not readily find close by a support up which to twine; whereas later, there is seldom any lack of annual stems or shoots of perennial plants in the immediate neighbourhood.

When the twisted embryo germinates, it stretches and at the same time revolves from right to left, assuming the shape of a screw and pushing its lower clavate extremity out beyond the coat of the seed (see fig. 34<sup>1,2,3,4,5,6</sup>). This extremity forthwith grows into the earth and fastens tightly on to particles of the soil, withered foliage, and other objects of the sort. The other, attenuated extremity of the filiform seedling, which is still wrapped in the seed-coat and the mass of reserve-food, lifts itself up in the opposite direction, avoiding such solid bodies as it may happen to encounter, and grows in a curve round them. Further growth does

not take place at either extremity, but always in the median part of the filament. It is so rapid that by the fifth day after the commencement of germination the entire seedling has increased fourfold in length. As early as the third day after the emergence of the tip that fastens itself in the earth, the integument of the seed, which until then continues to envelop the opposite extremity, is thrown off and the seedling's apex is exposed. The reserve-food, given by the parent-plant to the seedling as provision for the journey, has meanwhile been absorbed and consumed, so that the seedling is now thrown entirely upon its own resources, and depends for sustenance upon the earth, to which it is firmly attached, and upon the surrounding air. Having no chlorophyll, it is not in a position to take up

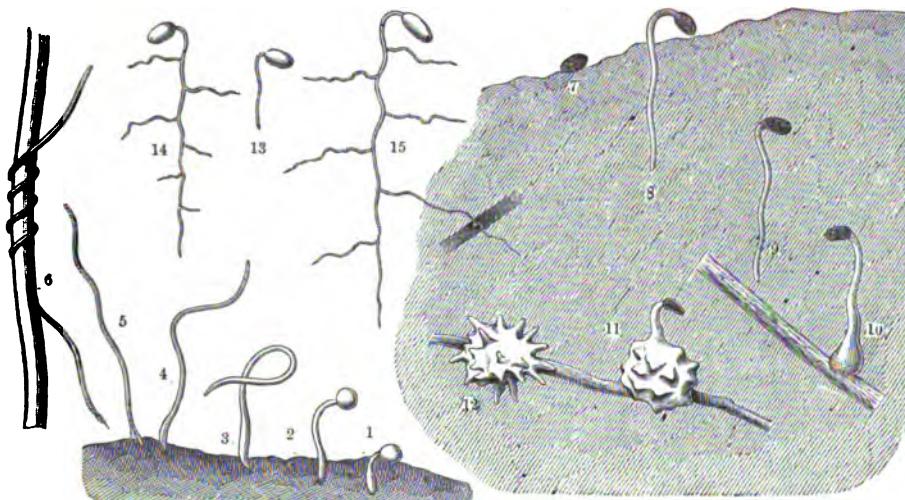


Fig. 34.—Seedlings of Parasitic Plants.

1, 2, 3, 4, 5, 6 The Great Dodder (*Cuscuta Europaea*). 7, 8, 9, 10, 11, 12 A Broom-rape (*Orobanchus Epithymum*).  
13, 14, 15 Wood Cow-wheat (*Melampyrum sylvaticum*).

materials from the air; nor can it derive sufficient nutriment from the earth, even supposing that water is imbibed by the cells of the clavate extremity. There is no doubt that it now grows at the expense of the substances contained in the cells of this club-shaped end. The latter at once begins to shrivel and soon dies, whilst the upper part of the filament elongates conspicuously. Should this portion of the seedling meantime come into contact with a neighbouring plant, a rigid haulm, or anything else that will serve as a support, it straightway coils itself round the object in question, and its future is then, as a rule, assured.

Failing such a support, the seedling, after the death of the clavate extremity, falls down and sinks to the ground. In doing so, it almost invariably touches an adjoining object, whereupon it immediately winds tendril-like round the support thus afforded. But if there is nothing anywhere around to serve as a prop, and the young seedling, by this time from 1 to 2 centimeters long, comes to rest upon the bare earth, all further growth is stopped. It preserves its vitality, however, for a surprisingly long time, and may remain almost unal-

tered, lying on the damp earth for four or five weeks waiting for something to turn up. Not infrequently something of the sort happens, for another plant may germinate close by or extend a growing shoot from the vicinity and touch the *Cuscuta* seedling. In this event, the latter at once seizes the anchor thus thrown out, and winds round it. But if no support of the kind is to be had, the seedling must ultimately perish. It is, to say the least, a very remarkable thing that a filament, capable of developing suckers when adherent to a living plant, is not able in damp earth to produce any absorbent organs whatsoever.

If the thread-like Dodder plantlet succeeds in seizing a support of any kind, either during the existence of the swollen extremity, or later, after it has been absorbed, it makes a single, or from two to three, coils round the prop, raises its growing point from the substratum, and moves it round in a circle like the hand of a watch. By means of these manœuvres, which look exactly like a process of feeling or seeking, the filament is brought into contact with fresh haulms, twigs, and petioles belonging to other plants. To these it adheres, making once more two or three tight coils round them. Throughout, it is obvious that the growing point of the young Dodder rejects dead props, as far as is practicable, and shows a striking preference for living parts of plants.

At each place where the Dodder is pressed in a coil against the support, the filament becomes somewhat swollen, and wart-like suckers are developed, which are usually situated close together in rows of three, four, or five (see fig. 35<sup>1</sup>).

A piece of stem thus furnished with suckers or haustoria resembles a small caterpillar creeping up the supporting stem. These haustoria, arranged close together in rows, and corresponding in origin entirely to rudimentary roots, are at first smooth, but acquire soon a finely-granulated aspect owing to the walls of the epidermal cells projecting outwards. With the help of the papillæ thus formed, and especially through the action of a juice secreted by them, the suckers fasten themselves to the host. If the plant has been obliged to clasp a dead object for support, the wart-like processes flatten themselves against it and assume the form of a kind of disc, which exhibits no further development, and only serves as an organ of attachment; but, if the substratum is a living plant, a bundle of cells forces its way out from the middle of the haustorium and grows into the substratum direct. The phenomenon here manifested is altogether characteristic. Each sucker from the time of its production exhibits a kind of core composed of cells arranged in regular rows, which, together with a few spirally-thickened vessels, constitute a bundle standing at right angles to the axis of the Dodder's stem. This bundle now breaks through the coat formed by the rest of the cells of the sucker and penetrates into the living tissue of the plant attacked (see fig. 35<sup>2</sup>). Great force is exerted in the penetrating process. The closely-joined cells of the epidermis, and not infrequently a cortex of considerable density are pierced, and the bundle of cells often penetrates right into the body of the wood. Having once reached the interior of the host, the cells, till then bound together in a bundle, diverge a little, insert themselves singly between the cells of the host,

and energetically absorb food-materials. They withdraw organic compounds from the host and convey them by a short route to the strands developed meantime in the axis of the *Cuscuta*-stem. When once a union of this kind between the parasite and the host has been established, the portion of the *Cuscuta* situated below the first haustorium gradually dies. The lowest extremity, *i.e.* the clavate tip, has already perished, so that the *Cuscuta*-plant is now no longer in any connection with the ground whereon it germinated, but only remains rooted to its living host by means of the suckers. If it has had the good fortune to cling to a host with green foliage, which generates an abundance of organic compounds, such as the luxuriant juicy stems of the Hop, or the Nettle, with its

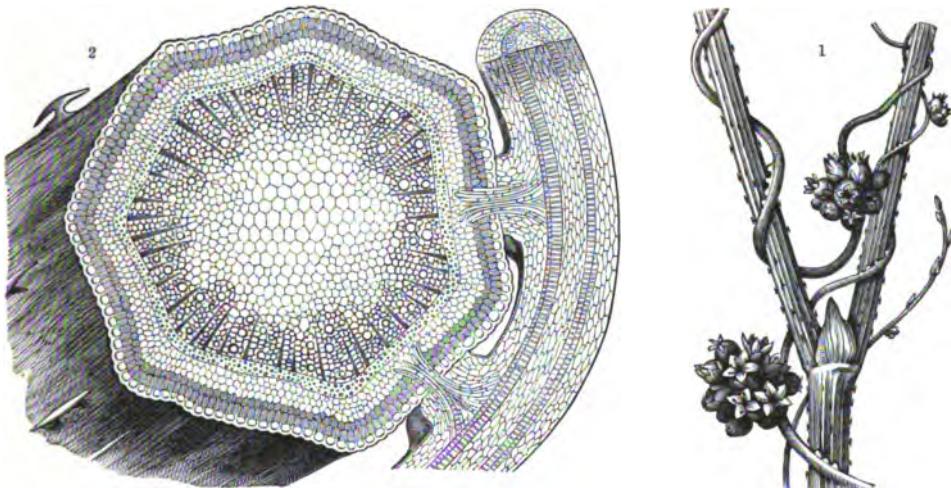


Fig. 35.—*Cuscuta Europaea* parasitic on a Hop-stem.

1 Natural size. 2 Section;  $\times 40$ .

plentiful dark green leaves, which are shunned and spared by grazing animals on account of their unpalatable stinging hairs, the parasite continues to grow with extraordinary rapidity, and puts forth a number of branches immediately above the lowest group of haustoria. All these again feel around with their tips, develop tendrils and suckers, sometimes intertwining and becoming entangled together, cover an ever-increasing area of the host with their network, and in this condition fully deserve the name of "Hell-bind", sometimes popularly applied to this plant. Little spheres of rose-coloured flowers are then formed on individual threads of this tangle, and from them balls of small capsular fruits, which dehisce by means of lids and have their seeds shaken out by the wind.

The European species of *Cuscuta* are all annuals. Even when their haustoria are attached to perennial plants, as, for instance, on young branches of woody plants, they wither after the seeds have ripened, and nothing is to be seen of them in the following spring except a few dried tendrils coiled round branches of ash or willow. But under a tropical sun, perennial species flourish as well. The suckers of *Cuscuta verrucosa*, for example, continue to exercise their function

throughout the year wherever they have once attacked the host. If the woody branches of the host, with haustoria fastened in them, grow in thickness and superimpose new wood-cells upon the wood, down to which the absorbent cells of the haustoria have penetrated, these suction-cells of the Dodder are likewise inclosed by the wood-cells, and, in proportion to the augmentation of the circumference of the wood in the branch in question, they also lengthen out so that the bundle of absorption-cells proceeding from a sucker may, in such cases, be seen imbedded in the wood to a depth of several annual rings.

The *Cassytha*, referred to above, behave exactly like the Dodders. In them also the seedling which issues from the seed is filiform, and lives originally at the expense of reserve-food stored up within the coat of the seed. So, too, it grows upward, ramifies, and endeavours, by means of revolving movements of the apex, to reach a living support, coils round the latter when found, and uses it as a nutrient substratum. Here, again, at the parts where the tendrils of the filiform stem are firmly appressed to the living support, rows of wart-like suckers are developed, and a bundle of absorption-cells grows from each into the host. As in the Dodder, the lower extremity of the filiform stem then dries up at once, and connection with the earth is thus cut off. The parasite, once attached by its haustoria to the host, is able to branch repeatedly, to weave its thread-like stems over all the branches and to climb to the top of the host, even should the latter be a tall bush. At some spots everything is entangled to such an extent that one would think there were birds' nests amongst the boughs.

The second series of parasitic Phanerogams consists of herbs bearing green foliage-leaves, whilst the seed contains an embryo furnished with seed-leaves (cotyledons) and root. The seeds germinate in the earth and there develop seedlings without the support of a host; it is branches of the root that first attach themselves by means of suckers upon the roots of other plants. To this series belong about a hundred Santalaceæ, mainly of the genus *Thesium*, and many more than two hundred Rhinanthaceæ besides. The chief examples of this latter family are the various species of the Eyebright (*Euphrasia*), the Yellow-rattle (*Rhinanthus*), Cow-wheat (*Melampyrum*) and Lousewort (*Pedicularis*), and also *Bartsia*, *Tozzia*, *Trixago*, and *Odontites*. The most extensive genera are *Euphrasia* and *Pedicularis*, the species of which, with few exceptions, are found in the northern hemisphere, adorning grassy meadows with their pretty flowers, especially in the arctic zone, and the high mountain regions of the Himalaya, the Altai and Caucasus, the Alps and the Pyrenees.

Little suggestion of parasitic habit is given in the first stages of development of any of these plants. A seedling of the Cow-wheat within a week puts forth a primary root 4 cm. long, from which half a dozen lateral roots ramify at right angles without there being any attachment to a host to be noted (see fig. 34 <sup>13, 14, 15</sup>). Suckers are never developed until the secondary roots have attained a length of from 12 to 24 mm., and then only if the latter come into contact with other living plants to their taste, a circumstance which doubtless is almost certain to happen,

seeing that the lateral roots are numerous and are sent out in all directions from the main root, and therefore must inevitably come across the root-systems of other plants.

The seedling in perennial species of *Thesium* develops comparatively slowly. It reaches a length of from 3 to 4 cm. in the first year, sends a tap-root into the earth, and puts forth a few branchlets, which do not fasten upon the roots of other plants by means of suckers until several weeks after germination. These suckers are relatively large in all species of *Thesium*, and they catch one's eye the moment the roots of a plant are carefully divested of earth. They are then recognized, as may be seen in fig. 36<sup>1</sup>, as little white knobs, which stand out clearly from the dark earth and are always inserted laterally upon the secondary roots. They are

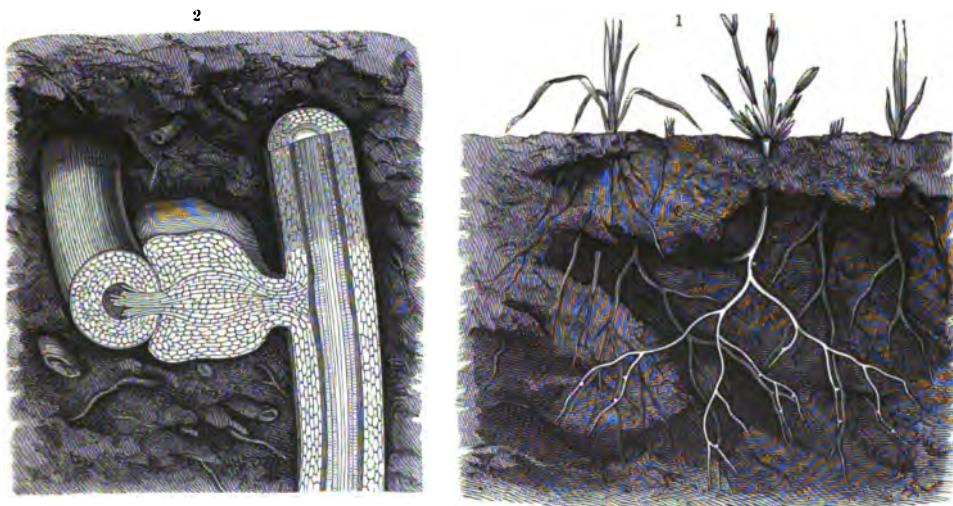


Fig. 36.—Bastard Toad-flax (*Thesium alpinum*).

<sup>1</sup> Root with suckers; natural size. <sup>2</sup> Piece of a root with sucker in section;  $\times 35$ .

constricted near their insertion, and the strangulated portion often gives the impression of being a pedicel upon which the knob is seated. This knob is differentiated into a central core and a multicellular, cortical coat enveloping it. The cellular coat rests upon the root of the host attacked, and does not merely adhere to one limited spot, but spreads itself out over the root like a plastic mass, and forms a cushion surrounding about a fourth or fifth part of the circumference (see fig. 36<sup>2</sup>) without, however, penetrating into the substance of the root. There are in the core two strands or bundles of vessels, and between them small cells arranged in rows, from which absorption-cells arise at the spot where the sucker first applied itself to the nutrient root. These absorption-cells grow out beyond the rind-like envelope round the core, perforate the cortex of the host, penetrate into the wood at the centre of the invaded root, and there diverge like the hairs of a dry paint-brush.

The suckers of the green-leaved Rhinanthaceæ are on the whole similarly constructed; only they are relatively smaller and more delicate, being sometimes almost translucent, and they are either not at all or only slightly constricted at the

base. Whereas in *Thesium* they never issue otherwise than laterally from the ramifications of the roots, in Rhinanthesæ they are often terminal. A differentiation into core and rind-like envelope is never clearly marked; a vascular bundle runs through the middle of the sucker and is surrounded by thick-walled cells. The absorbent cells are, moreover, shorter than in the Santalaceæ. The individual genera of the Rhinanthesæ exhibit amongst themselves only very slight differences in respect of their suckers. On the roots of Eyebright (*Euphrasia*), the haustoria are tiny roundish nodules which rest upon the host's root without encompassing it. The absorption-cells are very short, and only just penetrate into the host. The vascular bundle is either entirely wanting within the sucker, or its place is taken by a single, comparatively large vessel. On the roots of the Yellow-rattle (*Rhinanthus*) the suckers are spherical and of considerable size (up to 3 mm. in diameter); their margins are swollen and often encompass more than half the circumference of the roots attacked. The absorbent cells are short but very numerous. In the Cow-wheat (*Melampyrum*) the suckers resemble those of the Yellow-rattle in size and shape and in the shortness of the absorption-cells; but in the former the margins of the suckers not only embrace the roots of the host, but cling to them in such a way as to penetrate their substance and form circular grooves upon them.

All the Rhinanthesæ mentioned are herbaceous annuals. Their suckers are few in number, and therefore easily escape observation. By the time these plants ripen their seeds any piece of a root that has been attacked has for the most part already turned brown and been killed, and is in a state of decay. But shortly afterwards the parasite itself withers. The comparatively large seeds, well-furnished with reserve-material for the nourishment of the embryo, fall out of the dry capsules, and generally reach the ground at no great distance from the mother-plant and germinate there. In the autumn, close to Cow-wheat plants, which are still green but have already let fall the seeds from their lowest capsules, individual examples of those seeds may be seen already sprouting in the damp moss and mould on the ground of woods. If they fall to earth not very far from the parent-plant, the seedlings may happen to attack the host which has already had one of the branches of its root sucked and killed by the latter in the previous summer.

Nearly all these annual green-leaved parasites make their appearance in numbers close together. If, for instance, a species of Cow-wheat has taken up its quarters in a particular part of a wood, there are always collections of hundreds and thousands of specimens to be found together. The small-flowered Yellow-rattle often grows so abundantly in damp meadows that one might suppose it to have been sown by the bushel. The large-flowered, hairy Yellow-rattle is similarly exuberant in ploughed fields, and the Eyebright, with its large number of species, is produced in such abundance in mountainous districts that, at the season when its little milk-white flowers are open, regular milky ways seem to stretch across the green meadows. Millions of them are situated together rooted in the grass-covered ground, and one would suppose that in course of time the growth of

grass at such places would be injured. This conclusion appears to be supported by the assertion of the country folk that after the season when the Eyebright is in full bloom, the cows yield less milk, a fact which explains the German name of "Milchdieb" (milk-thief) popularly given to the plant. The diminution in the quantity of milk yielded is, however, certainly connected with other circumstances. It depends especially upon the universal abatement of the growth of grasses in early autumn and the consequent curtailment of the food afforded by the pastures. The injury done by the Eyebright to its hosts by the withdrawal of nutriment and destruction of rootlets cannot be very considerable, for the appearance of the grasses and other host-plants, which are affected, is not noticeably different from that of the plants of the same kind which escape invasion.

The same statement is true in the case of the various species of Lousewort (*Pedicularis*), almost all of which are meadow-plants; that is to say, they are present in great abundance in upland and alpine pastures without apparently injuring the species growing in their company and used by them as hosts. Unlike the species of Cow-wheat, Yellow-rattle, and Eyebright, however, nearly all the Louseworts are perennial, and accordingly differ from them also in the construction of their suckers. There is, it is true, no difference in shape between the suckers of the Cow-wheat and those of *Pedicularis*, but they are dissimilar in respect of size and place of origin. The suckers of the perennial Louseworts are barely more than half the size, and are only developed near the attenuated extremity of a rootlet. They are very few in number; each of the long, thick, fleshy rootlets, proceeding from the base of the stem usually produces a single sucker only which settles upon the root of a suitable host-plant in the same way as the suckers of Cow-wheat. By the time that the parasite's fruit ripens, the piece of root which has been invaded has usually already turned brown and fallen into decay. Now in the case of Cow-wheat it may undoubtedly be immaterial whether the piece of root attacked by it is living or not when its fruit is ripening, inasmuch as its own annual root rots as soon as the seeds have been produced from the flowers above ground. But with *Pedicularis* it is different. The perennial roots of this plant require a host to nourish them next year, and when the piece of a host's root which has been attacked and sucked as a nutrient substratum one year dies, the sucker belonging to the root parasitic upon it is no longer in a position to fulfil its function by continuing to absorb fresh juices. Suckers thus reduced to a state of quiescence soon perish, and only leave little scars to indicate the places where they existed. The perennial root of the *Pedicularis* has now to seek a new source of nutriment, and this is effected by the elongation of its tip, which continues to grow until it reaches the living root of another plant suitable as host, whereupon it develops a fresh sucker upon that root. This elongation doubtless requires a large quantity of plastic materials; but these are found stored in abundance in the older parts of the parasitic root.

These circumstances explain, at anyrate in part, the characteristic structure and disproportionate length of the roots of *Pedicularis*. From all round the short erect

root-stock, which is generally only from  $\frac{1}{2}$  cm. to 2 cm. long, issue fleshy rootlets of the thickness of a quill, but, in many species, as long and thick as a little finger. These rootlets are abundantly supplied with starch, and, in course of time, elongate till they measure 20 cm. They radiate in all directions in the black soil of the meadow, wherein are buried the root-systems of grasses, sedges, and various other plants, and fasten on to suitable hosts by means of one or two suckers yearly, and repeating this process until at length their tips travel into earth devoid of roots, where no more prey is to be found, and there growth ceases. This explains also why these long *Pedicularis*-roots never descend vertically in the earth, but remain only in the upper strata of soil on a meadow, where a number of other roots are interwoven together, and where it is most likely that the tapering growing-point will meet with the root of some new host or other.

The Alpine *Bartsia* (*Bartsia alpina*), one of the perennial Rhinanthesæ prevailing in the arctic regions as well as in mountainous parts of Europe on damp, marshy, grass-covered spots, is distinguished by the sombre dusky violet colouring of its leaves, and has already been noticed amongst carnivorous plants. On the secondary roots are suckers exactly like those of the Yellow-rattle (*Rhinanthus*), and by means of these organs it clings to the fibrous roots of sedges and grasses, and sucks their juices. The long, subterranean, runner-like stems, which are covered with small, whitish scales, also bear, however, elongated absorption-cells (root-hairs), which are distinctly differentiated, and take up nutriment from the vegetable mould around. This *Bartsia* is, therefore, half-parasitic and half-saprophytic, and it is not improbable that many other perennial Rhinanthesæ behave in the same way.

The species of *Pedicularis* which constitute the most extensive group of perennial green-leaved and parasitic Rhinanthesæ are, it is true, destitute of tubular absorption-cells (root-hairs) whether on the subterranean stem-structures or on the root-tip, with the exception of those which develop in the middle of the suckers. But the construction of the epidermal cells on the roots, and the circumstance that these epidermal cells are always in intimate connection with dark particles of humus, would favour the idea that these plants are capable of taking up organic compounds from the mould of meadows in addition to the food acquired by means of suckers from their hosts. This supposition is further supported by the fact that I succeeded in rearing a species belonging to the Rhinanthesæ, namely, *Odontites lutea*, from a soil composed of a mixture of sand and humus, in which no other plants were rooted, so that the possibility of a withdrawal of nutritive matter from hosts was excluded. It is true that the plants thus reared remained comparatively small and poor, and only developed few flowers and fruits. But at anyrate they may be considered to prove that plants exist, which, though normally parasitic, are yet on occasion able to subsist in vegetable mould without the assistance of hosts.

The third series of parasitic flowering-plants is very restricted, contrasting in this respect with the second series, composed of the numerous green-leaved Santalaceæ and Rhinanthesæ. The species belonging to it differ from those of the

second series chiefly in their lack of chlorophyll. They all live underground on the roots of trees and shrubs, develop deep down in the earth a number of flowerless perennial shoots thickly covered with scales, and, in addition, push up annually into the light temporary axes bearing flowers, which ripen their fruits and die after the fall of the seed.

As the best known representative of this series, we may take the Toothwort (*Lathraea Squamaria*), which is represented in fig. 37, and has been already described on a previous occasion as an instance of a plant nourished by capturing

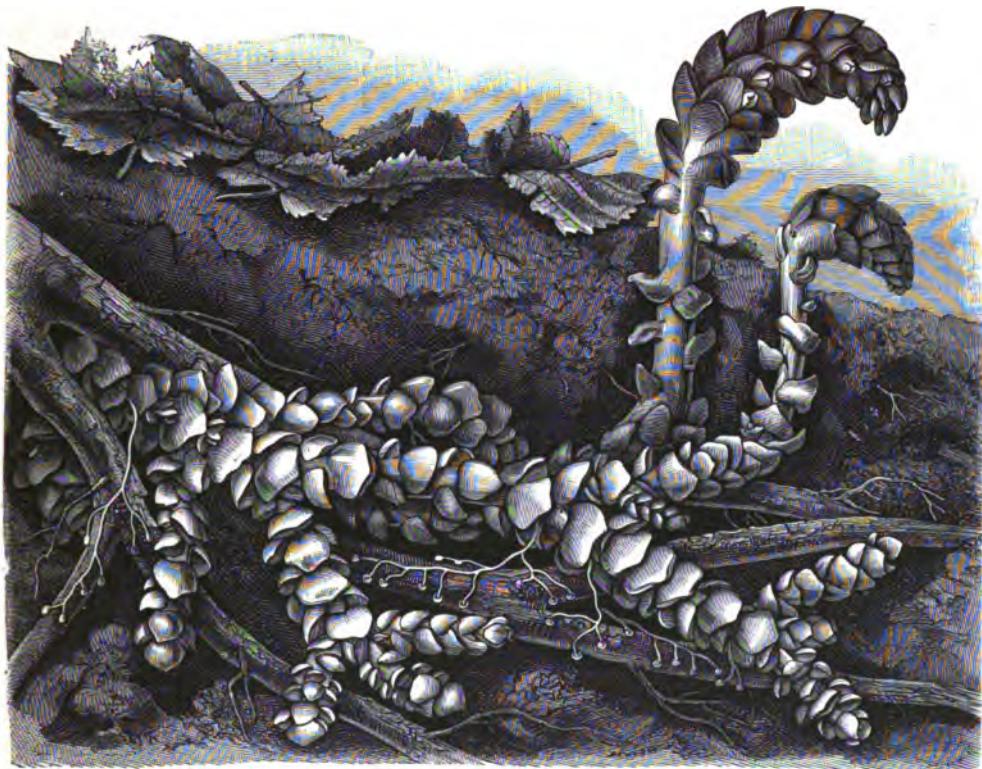


Fig. 37.—Toothwort (*Lathraea Squamaria*) with suckers upon the roots of a Poplar.

and digesting infusoria in special receptacles. Like *Bartsia*, it is a remarkable example of a plant living on juices in part derived from animals killed by itself and partly from living hosts. Formerly, the Toothwort used to be included in the family of Broom-rapes (Orobanchæ) on account of the structure of its capsules, but it is entirely different as regards the form of its seedling. For, whereas the seedling of a Broom-rape is a thread without any trace of cotyledons, as will be seen when we study its development and mode of attachment to the host in the next few pages, that of the Toothwort is clearly differentiated into radicle, cotyledons, and rudimentary stem, corresponding in this respect entirely with the Rhinanthonchaceæ. Moreover, the Toothwort resembles Rhinanthonchaceæ much more than Broom-rapes in the manner in which it attacks its hosts and withdraws nutriment from them.

The seed of *Lathraea* germinates on damp earth. The young root of the seedling grows at first at the expense of reserve material stored in the seed, penetrates vertically into the earth and sends out lateral branches, which, like the main root, follow a serpentine course and search in the loose damp earth for a suitable nutrient substratum. If one of these meets with a living root belonging to an ash, poplar, hornbeam, hazel, or other angiospermous tree, it fastens on to it at once and develops suckers at the points of contact; these suckers are at first shaped like spherical buttons, but soon acquire, as their size increases, the form of discs adherent to the host's root by the flattened side and with the convex hemispherical side turned towards the rootlet of the parasite. These discoid suckers cling to the root attacked by means of a viscid substance produced by the outermost layer of cells. As in the case of the parasites already described, a bundle of absorption-cells grows out of the core of each sucker into the root of the plant serving as host, and the tips of the absorbent cells reach to the wood of the root. The shoot extremity of the seedling, thus nourished by the juices of the host, now develops very quickly, elongating and producing thick, white, fleshy, scale-like leaves which overlap one another closely, the whole thus acquiring the appearance of an open fir-cone. The scaly stems also branch underground, and thus a curious structure is gradually produced, consisting of crossed and entangled cone-like shoots covered with white scales, and this structure fills entirely the nooks and corners between the woody roots on which it preys. Individual plants extending over a square meter and weighing 5 kilograms are by no means rare. Later on, inflorescences raise themselves above the surface from the extremities of the scaly subterranean shoots. Their axes are at first curved like crooks, but straighten themselves out by the time the fruit ripens. Whereas the subterranean portions are white as ivory, the flowers and bracts pushed up above the earth are of a purplish tinge. The roots, which issued originally from the seedling, and their suckers have long since ceased to meet the requirements in respect of nourishment of so greatly augmented a structure, and therefore additional adventitious roots are produced every year, springing from the stem and growing towards living woody branches of the thickness of a finger, belonging to the root of the tree or shrub that serves as host. When there, they bifurcate, forming numerous thickish filiform arms, which lay themselves upon the bark of the nutrient root and weave a regular web over it. Sometimes two or three of these root-filaments of the parasite coalesce, forming tendrils, and the resemblance to a lace-work or braid is then all the more pronounced. Suckers such as have been described are developed by these root-filaments laterally, and more especially on the ends of the branches.

*Lathraea* is interesting in so many different connections that we shall again return to this plant later on. As has been stated before, it affords a type of a series of parasites which resembles the species of *Cassytha* and *Cuscuta* in the absence of chlorophyll, Rhinanthaceæ in the shape and development of the seedling and the form of the suckers, and the Balanophoreæ, presently to be described, in being parasitic upon the roots of woody plants. *Lathraea Squamaria*, the species repre-

sented in fig. 37, is indigenous to Europe and Asia, its area of distribution extending from England eastwards to the Himalayas, and from Sweden southwards to Sicily. Two species are confined to the East, the Crimea and the Balkans, and another Toothwort (*Lathraea clandestina*), distinguished by large flowers, but slightly raised above the earth, extends in western and southern Europe from Flanders over France to Spain and Italy. This last has the distinctive feature that the discoid suckers developed on its yellow roots, which latter are of the thickness of a quill, are as large as lentils and the biggest hitherto discovered on any plant.

#### BROOM-RAPES, BALANOPHOREÆ, RAFFLESIACEÆ.

The fourth series of parasitic Phanerogamia is composed of plants destitute of chlorophyll, whose seed contains an amorphous embryo without cotyledons or radicle. The seed germinates on the earth, and the embryo grows as a filiform body into the ground and there fastens upon the root of a host-plant, penetrates into and coalesces with it in growth, forming a tuberous stock, from which, later on, flowering stems are projected above the earth.

To this series belong the Broom-rapes or Orobanchææ and the Balanophoreæ. Of the genus *Orobanche* about 180 species are recognized, which, exhibiting great uniformity in floral structure and in their general development, can only be distinguished by minute characteristics. The flowering stem growing up from the subterranean tuber is, in all the species, rigid, erect, thick, fleshy, and covered at the top with dry scales. The open flowers, ringent in shape, are crowded together in a terminal spike, and often emit a strong scent like that of pinks or sometimes of violets. The colour of the flowers is in one group (*Phelypæa*) mostly blue or violet; in the rest it is waxen yellow, yellowish-brown, dark-brown, rose-red, flesh-tint, or whitish. *Orobanche violacea* and *O. lutea*, both natives of Northern Africa, have stems which grow to a height of half a meter and become almost as thick as an arm. The best-known species is the Branched Broom-rape (*Orobanche ramosa*), which is parasitic on the roots of hemp and tobacco plants, and is very widely distributed. The greatest number of species belong to the East and to Southern Europe. The extreme north of America harbours one species which bears a single flower at the end of its stem. In all the species the stem projects only partially above the earth. The subterranean portion, adherent to the root of a host, is often greatly swollen and thickened above the place of attachment; in the case of *Striga orobanchoides*, which is prevalent in the Nile basin, it is irregularly lobed above the host's root. The root of the nutrient plant also is usually somewhat swollen wherever a parasitic *Orobanche* has settled upon it, and sometimes it exhibits an irregular outgrowth inclosing the spot whereto the *Orobanche* is adnate like a cup. Beyond the place of attachment of the parasite the root has often the appearance of having been bitten off, and this is owing to the fact that the particular piece of root has been killed and demolished by the attack of the parasite. From the base of the stem, near the point of adhesion to the host, spring short, thick, fleshy fibres, and

one or other of these bends its tip towards the root of the foster-plant and clings to it. These fibres are, in many species, very numerous, and are interlaced and entangled so as to form a reticulate mass, which vividly recalls that of the Bird's-nest, and is an instance of the general resemblance existing between Orobanchææ and the Orchidææ destitute of green leaves (*Neottia*, *Corallorrhiza*, *Epipogum*, *Limodorum*), which have already been discussed.

The establishment of parasitic Orobanchææ upon the roots of host-plants takes place in the following manner. The embryo imbedded in the small seed shows no trace of differentiation into root and stem, possesses no cotyledons, and indeed consists only of a group of cells; it is surrounded by other cells filled with reserve-nutritment. When this embryo grows forth from the seed, during which process it consumes the reserve-food, it exhibits no distinction between root, stem, and leaf, but is a spiral filament consisting of delicate cells. One extremity, the shoot end, of this filiform seedling, remains covered by the seed-coat, which looks like a dark cap (fig. 34<sup>8</sup>); the opposite extremity is the root.

The seedling Broom-rape stretches downwards just as the Dodder (*Cuscuta*) extends upwards. In so doing the descending tip traces a spiral line, and so, as it were, seeks in the earth for the root of a plant suitable as host. If the search is fruitless, and if the reserve-material in the seed has meantime been altogether consumed, the seedling begins to wither and gradually shrivels, turns brown, and dries up. It lacks the power of nourishing itself by means of the surrounding earth. But, if the lower, foraging extremity of the seedling succeeds in finding a live root belonging to a plant able to serve as host, it not only adheres closely to it, but swells in such a way as to give the young plantlet a flask-shaped appearance (fig. 34<sup>9</sup> and fig. 34<sup>10</sup>). The upper end is still inclosed by the seed-coat, but in proportion as the lower part thickens, the upper shrivels till no trace of it is left. The thickened part, on the other hand, which has become attached to the root of the host, becomes nodulated and papillose. Some of the papillæ develop into elongated conical pegs, and the young Broom-rape now rests upon the nutrient root in the shape of the head of a fighting-club (see fig. 34<sup>12</sup>). At the place of attachment one of the conical pegs has meanwhile penetrated the cortex of the root, and there it continues to grow energetically, forcing the cortical tissue apart, until it reaches the wood. Vessels now arise in the body of the young club-like plant, and, passing through the middle of the plug, wedged in the nutrient root, are brought into connection with the vessels of the latter. At the point of union between host and parasite, a bud is formed, clothed with abundant scales, which may best be likened to the bulb of the Martagon Lily. Lastly, out of this bud grows a strong, thick stem, which breaks through the earth and lifts a spike of flowers into the sunlight.

That portion of the Broom-rape which is buried in the root of the host-plant is so intimately associated with the separate parts of that root in the development of a tuber that it is usually difficult to determine which cells belong to the parasite and which to the host. The degree of union is such that one cannot even state with

certainty where the epidermis of the nutrient root ceases, and that of the Broom-rape begins. The latter looks as if it were a branch growing out of the root it preys upon, and this apparent fusion gave some colour to the view of the earlier botanists, who, ignorant of the life-history of these parasites, believed that they did not arise from seeds, but were pathological outgrowths of the roots, produced from their tainted juices; in other words, that they were "pseudomorphs" sprouting from diseased roots in the place of leafy branches.

It is also deserving of mention that some of the thick, fleshy fibres issuing laterally from the nodulated seedlings curve towards the host's root, bury their tips in the cortex, and thenceforth behave exactly like the peg which was inserted at the point where the seedling first became attached. We must leave undecided the questions as to whether the other fibres, which terminate freely in the earth, are capable of taking up food-materials from that source, whether these fibres are only present in perennial species and become the starting-points of new individuals, and lastly, whether they should be looked upon as root-structures or as stem-structures.

In addition, it is noteworthy that in many *Orobancheæ* only those embryos continue to develop which meet with a plant suitable to be their host. Although it is not the case that every species of *Orobanche* adopts one particular species of plant as foster-parent, yet thus much is certain, that most of them only thrive on members of a limited circle of species; one lives exclusively on kinds of Wormwood, a second on species of Butter-bur, and a third on those of Germander. For example, *Orobanche Teucrii* prevails on *Teucrium Chamaedrys*, *Teucrium montanum*, &c., the hosts being invariably species of the genus *Teucrium*. Suppose a hill thickly covered with plants comprising *Teucrium montanum* growing in company with thyme, rock-roses, globe-flowers, sedges, and grasses, but no great abundance of the *Teucrium*, a plant belonging to the species named occurring only here and there, and let *Orobanche Teucrii* have established itself at one particular spot, have attained to flowering and developed fruits, the tiny seeds of which have been shaken by the wind out of the ripe capsules. Owing to the exceptional minuteness and lightness of its seeds, every gust of wind will scatter them in innumerable quantities over the entire hillside and beyond it. The next step is germination. Filiform embryos emerge from the seeds, in the manner described above, and penetrate into the earth. *Teucrium montanum* being only sparsely present on the hill in question, comparatively few seedlings will meet with the roots of that plant, whereas thousands will fall in with the roots of the thymes, rock-roses, globe-flowers, sedges, and grasses. But, curious to relate, only those seedlings of *Orobanche Teucrii* which come into contact with the roots of *Teucrium montanum* establish themselves firmly, penetrate into them, and continue their development; whilst the numerous individuals which touch the roots of the thyme and other plants perish. This phenomenon can scarcely be explained in any other way than by the supposition that the roots of *Teucrium montanum* alone, by virtue of their special structure and quality, afford a suitable nutrient substratum, and therefore constitute centres of attraction for seedlings of *Orobanche Teucrii*;

and that the roots of the thyme, rock-roses, and other plants growing upon the hill side by side with *Teucrium montanum* do not share this property.

Whereas the Broom-rapes constitute a family of plants, the species of which, though very numerous, are so similar in the structure of flowers and fruit, in the history of their development and in the general impression they convey, that it is necessary to discover minute distinctive marks in order to be able to classify them with tolerable completeness, the *Balanophoreæ*, which, together with these Orobanchææ, belong to the fourth series of parasitic Phanerogams, are related to one another in a manner quite the reverse. Only forty species of them are known, but they are so various that, on the basis of the obvious differences, no less than fourteen genera have been distinguished, among which the forty species are fairly equally divided. In respect of distribution and occurrence they also contrast strikingly with both Broom-rapes and Rhinanthonaceæ. The Orobanchææ belong in particular to the Mediterranean flora, and to the East, and the Rhinanthonaceæ, as has been already stated, adorn chiefly sunny pastures in arctic regions and in mountain districts of the northern hemisphere. *Balanophoreæ*, on the other hand, are only found within a belt encircling the Old and New Worlds, which stretches little beyond the equatorial zone to the north or south, and they almost all inhabit the dark bed of primeval forests, where they are parasitic on the roots of woody plants, beneath a covering of vegetable mould.

The genus of *Balanophoreæ* named *Langsdorffia* is confined exclusively to tropical America. One of its species (*Langsdorffia Moritziana*) is found native in the damp forests of Venezuela and New Granada, where it is parasitic on the roots of palms and fig-trees; a second species (*Langsdorffia rubiginosa*) occurs in Guiana and Brazil in the region of the sources of the Orinoco, and a third, the most common of all (*Langsdorffia hypogaea*) represented in fig. 38, has an area of distribution extending from Mexico to the south of Brazil. They all avoid the hottest districts, remaining rather in cool regions; indeed the species first named has been found at an elevation of from 2000 to 3000 meters. Unlike all the rest of the *Balanophoreæ*, *Langsdorffia* exhibits a branched, cylindrical stock ascending from the place of attachment to the nutrient root, more or less felted externally, and before putting forth any flowers has a remote resemblance to a doe's antlers with their winter covering of downy skin. These stems are almost as thick as a little finger, have a fleshy consistence, and exhibit a clavate expansion at the base where they rest upon the root of the host. Many of those stems which bear the male flowers are 30 cm. long; those which bear the female flowers are usually somewhat shorter. They are all of a pale-yellowish colour; the thickly tomentose *Langsdorffia rubiginosa* looks as if it were covered with a yellowish velvet. At the extremity of each of the ramifications of the stem, which are often extremely short, having then the form of lobes or knobs, a bud is developed sooner or later in the lower cortical layer. This bud swells, bursts the outer layer of cortex, uplifts itself and grows out as an inflorescence between the four lobes formed by the cruciform rupture of the bark. The inflorescence is surrounded, like

the capitulum of a composite, by a whorl of imbricating scales, of which the lower are shorter and broader, and the upper longer, narrower, and pointed at the apex. These scales being stiff, somewhat shiny, and varying in colour from a waxy yellow to orange or red—in the case of *Langsdorffia Moritziana* brown-red,—the whole inflorescence has a vivid resemblance to certain immortelles, namely, the large species of *Helichrysum* occurring at the Cape. The inflorescences bearing male flowers are elongated and egg-shaped, those possessing only female flowers are shorter and capitulate. The seeds dropped from the nut-like fruits, which are pulpy internally, have no special integument. The embryo exhibits no trace of



Fig. 88.—*Langsdorffia hypogaea*, from Central America.

cotyledons or radicle, but consists of an undifferentiated group of cells which may be likened to a tiny bulbul.

Seeds of this kind germinate like those of *Lathraea*, and upon meeting with the root of a tree or shrub suitable for prey, develop into larger tubercles and have a remarkable effect upon the substratum. The cortex of the host-root is destroyed at the place of adhesion of the tubercle, and its wood is laid open, lacerated, and unravelled. The woody bundles are diverted from their previous direction, ascend towards the parasitic tubercle, which meantime has grown into a full-sized tuber, and spread out like fans. The cells and vessels of the parasite penetrate between the ascending wood-fibres, and this results in the formation of a zone at the place of union of the parasite and root, where cells and vessels belonging to both interlace, traverse, and join one another, coalescing completely in exactly the same way as happens in the case of the species of Toothwort. A similar phenomenon occurs also when one of the wavy stems of *Langsdorffia* comes into contact with a root adapted to the purpose. The cortex of the root is demolished at the place of

contact; the wood is exposed, split open, and unravelled, whilst the tissue of the parasitic stem fills up all the interspaces in the upcurved and sundered woody bundles and fibres, and so intimate is the union thus effected that the stem of the *Langsdorffia* might be taken to be a branch of the root of the host-plant which sustains it. At the point of connection of an already adult *Langsdorffia* stem, the hypertrophy of the tissue is not very striking; but the base of each stem of an individual produced from a seed presents a highly swollen and clavate appearance. At first the parasite is only fastened by one side of this thickened base to the nutrient root, but later on it wraps both sides round the root, and rests upon the latter like a saddle on the back of a horse.

Between the bundles of a *Langsdorffia* stem there are passages filled with a peculiar wax-like matter named balanophorin. The quantity of this substance is so great that if one end of a stem of *Langsdorffia* is lighted, it burns like a wax-taper, and in the region of the Bogota these *Langsdorffias* are collected and sold under the name of "siejos", and are used for illuminating purposes on festive occasions. In New Granada they have also been employed in the making of candles; and, although this source of wax is not sufficiently abundant for us to be able to believe in its consumption and conversion on a large scale, the fact of its application in this manner shows that the parasite we are discussing must occur in great exuberance in many tracts of country in Central America.

Much rarer than the parasitic *Langsdorffias* are the species belonging to the genus *Scybalium*. Like the former these are confined to the equatorial zone of America. Two species, viz. *Scybalium Glaziovii* and *S. depressum*, flourish in mountainous districts, one of them indeed occurring only on the mountains of New Granada; two other species (*Scybalium jamaicense* and *S. fungiforme*) live in the woods and savannahs of lower-lying regions. The aspect of the last-named species when seen growing on the ground of a primeval forest, tempts one to suppose it to be a fungus, and it is easily understood why the first discoverer selected the term *fungiforme* to apply to it. Figure 39<sup>1</sup>, representing this rare and marvellous plant, is taken from the original specimens discovered in the year 1820 by Schott in the Sierra d'Estrella of Brazil, and brought thence by him to Vienna. We see that, in this case, instead of the elongated, wavy, branched stem characteristic of *Langsdorffias*, a lumpy, tuberous mass rests upon the root of the host-plant. This tuber is sometimes rounded and sometimes compressed and discoid; it is nodulated and often irregularly lobed also, and grows to the size of a fist. It is developed from a seed which, as is the case in all *Balanophoreæ*, is a cellular structure without integument containing an embryo destitute of cotyledons and radicle, and is best described as a minute tubercle. The embryo, after emerging from the seed and finding the living root of a woody plant, increases in volume, and, in the form of a little knob the size of a pea, exercises the same influence on the plant preyed upon as has been noted in the case of *Langsdorffia*. The root attacked is stripped of bark at the place where the tubercle is attached; the wood is then resolved into a fringe of fibres which stand straight up, and, diverging like the spokes of a fan,

distribute themselves in the tissue of the parasite, the latter having in the meantime developed into a tuberous stock as large as a nut. These radiating bundles, issuing from the wood of the nutrient root, come then into such intimate connection with the vessels formed in the tuber of the parasite, that the one appears to be a continuation of the other. They are, besides, entangled together, and between them is intercalated a mass of small parenchymatous cells which also adheres to the yet unfrayed portion of the foster-root's wood, and coalesces with it. The tuberous body of the parasite, which in the first instance is only adnate to the host on one

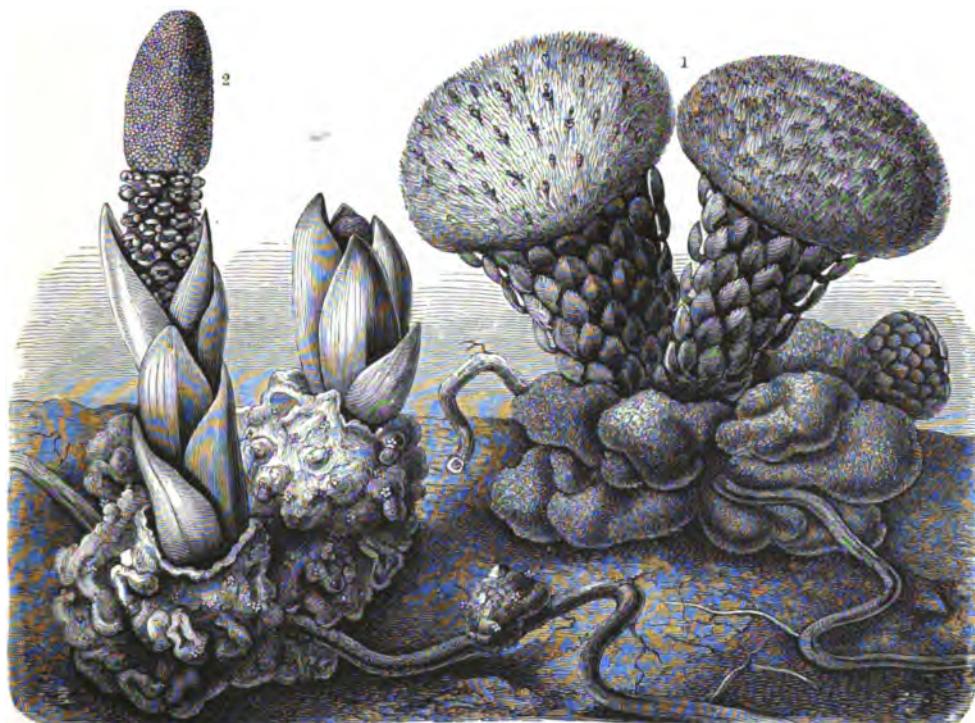


Fig. 39.—Parasitic Balanophores.

*1 Scybalium fungiforme*, from Brazil.

*2 Balanophora Hildenbrandtii*, from the Comoro Islands.

side, gradually encompasses it entirely, and the nutritive root then appears to perforate this irregular tuber. The inflorescences are produced direct from buds, which are formed under the bark at projecting spots of the brown tuberous stem, the cortex bursting open and allowing a thick flesh-coloured shoot, closely beset by ovoid pointed scales, to emerge and grow up into a form resembling a mortar-pestle. At the summit this shoot expands into a disc, and upon this are borne little capitulate groups of flowers, which are inserted amongst innumerable quantities of scales and hairs. The pistillate and staminate flowers are separated in different inflorescences, whilst the entire structure has an undeniable resemblance when in bloom to the inflorescence of an artichoke gone to seed, and later on to a toad-stool.

In the eastern hemisphere we find the various species of the genus *Balanophora* replacing the Langsdorffias and *Scybalia*. One of these, *Balanophora Hilden-*

*brandtii*, which is represented on the left side of the figure 39, occurs in the Comoro Islands off the east coast of Africa; seven species inhabit the islands of Java, Ceylon, Borneo, Hong-Kong, and the Philippines, and three species the East Indies. *Balanophora fungosa*, first discovered by Forster, is parasitic on the roots of *Eucalyptus* and *Ficus*, and is indigenous to Australia and the New Hebrides. The more elevated regions of Java and the Himalaya abound especially in these singular organisms. *Balanophora elongata* is so prevalent in Java on mountains of between 2000 and 3000 metres, that it is collected in quantities for the sake of the wax-like matter obtained from it. In that island candles are made from Balanophoras as they are from Langsdorffias in New Granada, or else rods of bamboo are smeared with the viscid substance, as they are then found to burn quite quietly and slowly. In the Himalaya, *Balanophora divica* or *B. polyandra* are the commonest and most widely distributed species, and *Balanophora involucrata* is there met with upon the roots of oaks, maples, and araliads even at a height of from 2300 to 2500 metres above the sea-level. They possess in almost all cases very vivid and conspicuous colouring—deep-yellow, purple, red-brown or flesh-tint, thus resembling the Gastromycetes, Clavariæ, and Toad-stools, in whose company they grow, and with which they manifest an additional uniformity in being all of fleshy consistence and containing no trace of chlorophyll. At a certain distance, moreover, the inflorescences rising from the dark ground in a wood, have the appearance of fungi, and all the early observers describe these Balanophoreæ with one accord as truly abnormal growths, viz. as fungi which by some marvellous accident bear flowers. They were also the object of the boldest speculations and most exuberant imagery on the part of the botanists belonging to the school of the "nature philosophers" of the first decades of this century. Even as late as the forties a famous German botanist says of them: "They are in the position of a hieroglyphic key between two worlds, which intercept and evade one another in an infinite variety of ways, like dreaming and waking moments", and the worthy Junghuhn, who discovered several of these plants in Java, writes: "Those are words which we may hope will be rightly interpreted thousands of years hence. Their sublime truth affected me deeply. There, flowerless and leafless, stood the mysterious plants which afford an instance of the combination of special vessels in a stalk like that of Balanophoreæ with the fructification of imperfect Hypocreæ!"

A young *Balanophora* not in flower is not unlike a *Scybalium* in appearance at the corresponding stage of its development. It consists of an irregular tuberous stem, which rests upon the creeping root of a tree or shrub. The exterior of this structure, which sometimes attains to the size of a man's head, is uneven, and in some cases convoluted like the human brain, or it may project in humps and knobs, or be divided into lobes or short branches like a coral-stem. The resemblance to the latter is heightened by the fact that the surface is covered by little papillæ shaped like stars or forget-me-nots, which distinguish the genus *Balanophora* from all allied genera.

The seeds settle upon the roots of trees, develop into tuberous axes, and unite with the nutrient root in the same manner as the *Balanophoreæ* already described. Also the inception of the rudimentary inflorescence beneath the cortex of the tuber and its eruption are similarly accomplished. In this genus the cortical layer thus broken through and forced outward always forms a large cup-shaped or crateriform sheath with an irregularly-lobed margin surrounding the base of the inflorescence.

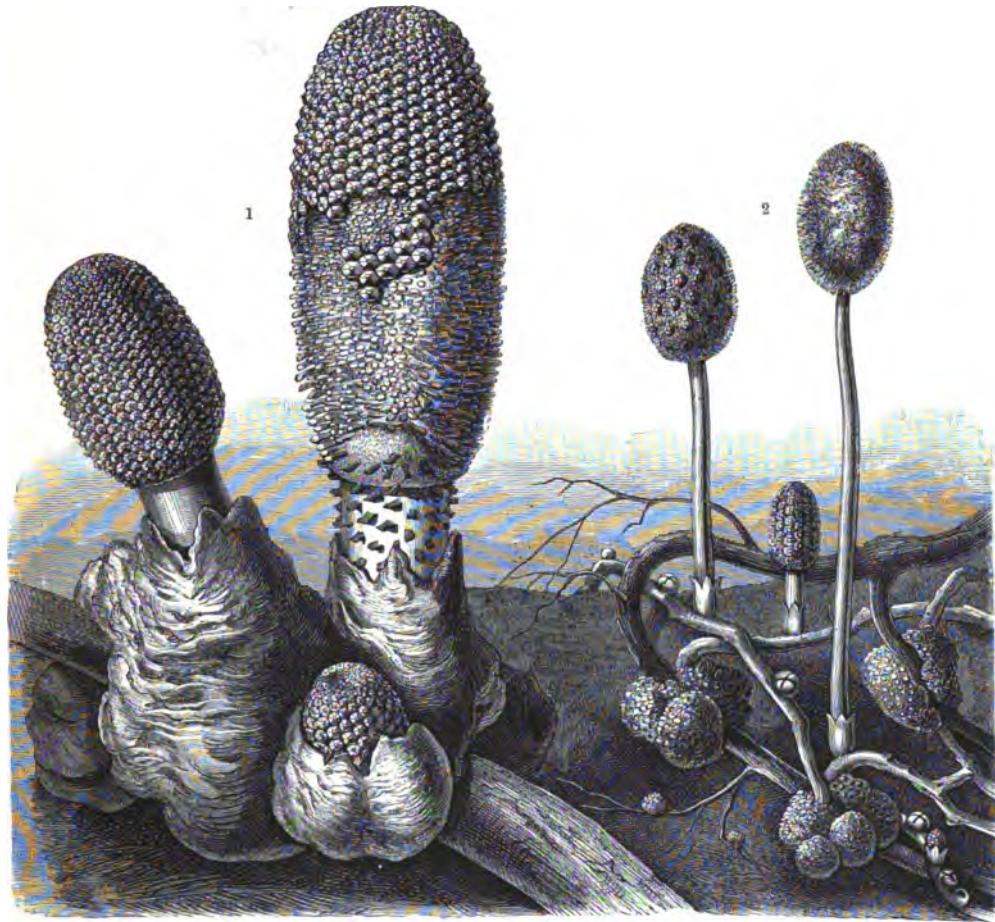


Fig. 40.—Parasitic Balanophores.

<sup>1</sup> *Rhopalocnemis phalloides*, from Java.

<sup>2</sup> *Helosis gujanensis*, from Mexico.

The inflorescence itself is spadiciform, and is borne by a thick shaft beset with large squamous leaves. The spadices growing from a tuber-stock are, for the most part, only as long as a little finger, but occasionally they reach a height of 30 cm., as, for example, is the case in the *Balanophora elongata* of Java, which is parasitic on the roots of *Thibaudia*.

The species of the American genus *Helosis*, whereof the most common (*Helosis gujanensis*) is represented above, resemble those of the genus *Balanophora* in the shape of the inflorescence. There is, however, considerable difference in the method adopted by these *Helosis* species of settling upon the roots of host-plants and in

the whole mode of growth. The phenomena of the swelling of the embryo into a tubercle after it has chanced upon a nutritive root, the destruction of the cortex, the exposure of the wood at that part of the root where the tubercle is adnate, and the derangement of the course of the woody bundles ensue, it is true, in the same manner as in the other *Balanophoreæ*; but the frayed wood-bundles of the foster-root only form quite short lobules which penetrate but a short distance into the parasitic tuber-stock, whilst the vascular bundles, formed meantime in the latter, adhere to them in such a manner that they might be mistaken for direct continuations of them.

When once the parasitic tubers have thus become adnate to a root, and by means of this union are provided with food, they grow round the nutrient roots in such a way that the latter appear to perforate or actually to issue from the tubers. They are always roundish, brown outside, and warty, but without scales, and they never produce inflorescences directly, but put forth in the first place several whitish or yellowish runners varying in thickness from a quill to a finger, which creep along horizontally under the ground, bifurcating, and becoming interlaced with other ramifications. At the places of contact they coalesce, and so occasionally form a net-work which is almost inextricably entangled with the root-system of the plant preyed upon. Whenever a runner of this kind comes into contact with a living root belonging to the host-plant, the surface of contact at once swells up. The part affected is converted into a tuberous mass and becomes adnate to the root, the process being the same as occurs in the case of the tubercle produced from seed. A net-work of runners thus connected with the root-system of the nutrient plant at several spots by means of tubers as large as peas might be compared to the reticulum woven by *Lathraea* round the roots of its hosts; but, apart from the size, there is the essential difference that inflorescences are never produced from the white threads of the ramifying and sucker-bearing roots of *Lathraea*, whereas the runners of *Helosis* afford points of origin for new inflorescences. Warts are produced on the surfaces of the thicker cylindrical runners, and within these are developed the buds of the inflorescences. The outer coat of the warts is then rent open at the top and constitutes a little cup, out of which grows a naked, scaleless shaft terminated by an oval spadix. Seeing that the runners rest horizontally under the earth whilst the shafts ascend bolt upright from the ground, the latter are always at right angles to the runners, of which they are to be regarded as branches.

The flowers are grouped in capitula, presenting in the spadix a dense mass. They are protected by peculiar bract-scales, each of which by itself is like a nail with a faceted head. These heads are in close contact with one another, so that the young inflorescence seems to be inclosed in a panelled coat of mail, and resembles to a certain extent a closed fir-cone. By degrees, however, these bract-scales detach themselves and fall off, and thus the flowers, till then roofed over by them, become visible. When the seeds are mature, the whole runner concerned in the production of the inflorescence, and usually also the tuber which served as the

starting-point of that runner, perishes, and another tuber belonging to the net-work above described, or rather the system of runners proceeding from it, becomes the basis for the development of new inflorescences. To this extent we may regard these *Helosis* species as perennial plants, whereas the majority of the other Balanophoreæ can lay no claim to this distinction, inasmuch as in their case the whole plant dies after it has flowered and ripened its seeds. The floral spadices in *Helosis* have a purple or blood-red colour, and in Brazil are called "Espigo de sangue". Only three species of *Helosis* have been discovered up to the present time, and those are distributed over equatorial America, in the Antilles, and from Mexico to Brazil.

Nearly allied to *Helosis* is the genus *Corynæa*, which resembles it in having facetted bract-scales like nails and a cone-like inflorescence, but differs entirely in other respects in its mode of growth, especially in being without runners. Four species of this genus have been discovered in the Andes of South America, in Peru, Ecuador, and New Granada, where they are parasitic, like the rest of the Balanophoreæ, upon the roots of trees. One of them, *Corynæa Turdiei*, is worthy of notice as living on the roots of Peruvian-bark trees, and is rendered conspicuous by its purple spadix, borne on a white shaft. *Rhopalocnemis phalloides* (see fig. 40<sup>1</sup>) is another root-parasite related to *Helosis*, and the single representative in Asia of these pre-eminently American groups. It is found preying upon the roots of fig-trees, oaks, and various lianes, in mountainous parts of Java and the eastern Himalayas, and is one of the biggest of all the Balanophoreæ. The fleshy, yellowish or reddish-brown tuber-stock attains to the size of a man's head; the inflorescences, which burst from the protuberances of this lumpy mass and are from two to six in number, are over 30 cm. long and from 4 to 6 cm. thick. The protuberances are light-brown in colour, and resemble in form a cycad-cone. *Rhopalocnemis*, a drawing of which is given in fig. 40<sup>1</sup> on a scale of one-half the natural size, is distinguished, like *Corynæa*, from *Helosis* by having no runners issuing from the tuberous axes.

The Lophophyteæ are set apart as a further group of parasitic Balanophoreæ, and differ from all the groups hitherto described in having their flowers arranged in separate roundish capitula upon a fleshy rachis springing from the tuberous-stock. They, again, belong to Central America, and are divided into three genera (*Lophophytum*, *Ombrophytum*, and *Lathrophytum*) into particulars of which we cannot enter without exceeding our limits. Only the genus *Lophophytum*, which is in many respects different from other Balanophoreæ, and in particular has been more thoroughly studied with reference to its peculiar mode of connection with the host-plant, demands special consideration. The *Lophophytum mirabile* (see fig. 41<sup>1</sup>) found in the primeval forests of Brazil adhering to the roots of Mimosæ, to those of Inga-trees especially, occurs at some places in such profusion that areas of ground, occupied by Inga-roots, from twenty to thirty paces in circumference appear to be entirely overgrown by the parasite. Hundreds of tubers, some large, some small, rest upon the roots of the trees, covered by fallen leaves and a light

stratum of vegetable mould. Most of them are the size of a fist, but a few are as big as a head, and then weigh 15 kilogr. and more. The tubercles formed directly by the germinating seeds which chance upon the roots are, by the time they attain to about the size of a pea, already in connection with the wood of the attacked root. The cortex and a portion of the wood at the place where the parasite is adnate are absorbed by this root. The tissue of the small tuber-stock is squarely and firmly inserted into the superficial notch thus made in the root, and short, peg-shaped bundles, isolated by the loosening of the wood of the nutrient root, appear to grow into the substance of the parasite. As the tuber increases in size vascular bundles are developed in it also, and these grow towards the said bundles of the host and unite with them.

No boundary can then any longer be certainly recognized between host and parasite, and the strangest fact of all is that we find, in these bundles, cells concerning which we are not able to decide, even by reference to their shape, whether they belong to the one or to the other. The cells which belong undoubtedly to the wood of the nutrient root have dotted walls; the bundles unquestionably developed in the parasitic tuber exhibit, on the other hand, cells with reticulate thickening, which, when slightly magnified, look as if they were transversely striated. Wherever these pitted and reticulate cells meet, cells are intercalated which do not altogether correspond either to the pitted variety belonging to the host or to the reticulate cells of the parasite, but display a form intermediate between the two. Here and there, too, cell-groups belonging to the parasite are entirely buried in the wood of the foster-root in its growth, and in the older tubers the cellular elements of the two plants there bound together are so involved that it is, as has been stated, impossible to establish any line of demarcation between the two.

By the time the tubers have reached the size of a fist their cortical layer is always solid, corky, and areolated; each of the areas being more or less uniformly angled, as is shown in the illustration below. Some of the more protuberant portions elongate and grow out into short, thick stumps bearing scales all round, each of the little areas having a triangular-pointed scale situated in the middle of it. At this stage of development the entire *Lophophytum* plant has an extraordinary resemblance to the squamigerous rhizome of a fern, or to a dwarf cycad-tree, stripped of its green leaves; and this likeness is enhanced by the fact that the bark and scales of *Lophophytum* are dark-brown in colour. From the centre of each of these thick stumps, which often reach a height of 15 cm., there now arises a spadiciform inflorescence. At first it is so thickly covered with ovate lanceolate scales possessing dark-brown, quasi-horny tips, overlapping one another like tiles, that the spadix as a whole looks extremely like an erect cycad-cone. Imagine the surprise of a traveller, who chances upon a spot in the depths of a primeval forest where the ground is occupied by *Lophophytum*, upon seeing hundreds of these brown, scaly cones grow up suddenly, in the course of a night following some days of rain, from the subterranean roots of the trees. A day or two later, this garden

of *Lophophyta* presents an altogether different picture. The brown scales have detached themselves from the rachis, first those at the base of cone, then also those on the upper parts. They fall off almost simultaneously, and with them the envelope which up to that time has concealed the flowers. The erect, fleshy, white, or reddish rachis bearing the flowers then becomes visible. The female flowers are

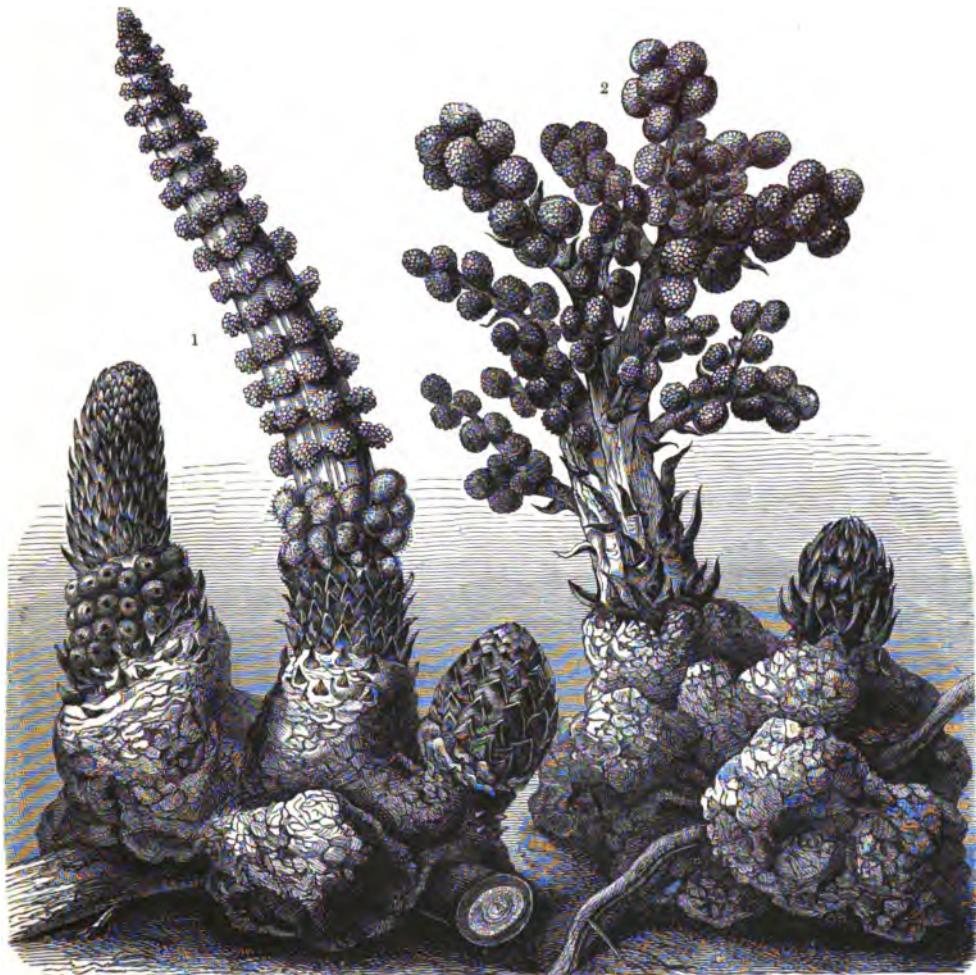


Fig. 41.—Parasitic Balanophores.

<sup>1</sup> *Lophophytum mirabile*, from Brazil.

<sup>2</sup> *Sarcophyte sanguinea*, from the Cape of Good Hope.

on the lower part, and arranged in spherical, deep yellow or orange-coloured capitula which are packed close together; the male flowers are situated above the lowermost third of the spadix, and are arranged in looser and less crowded capitula of a pale yellow colour.

However striking the phenomenon presented by these flowering cones of *Lophophytum mirabile*, it is surpassed by another native of Brazilian forests, the *Lophophytum Leandri*. The colouring of the inflorescence in this species cannot

be exceeded in variety, its rachis being pale reddish-violet, the bract-scales gamboge, the ovaries yellowish, the styles red, and the stigmas white. It is not surprising that even in Brazil, where there is certainly no lack of curious plant-forms, they have attracted attention, and that they are used there, as is the case with all rare plants, for purposes of healing and magic. The tubers of *Lophophytum mirabile*, which have a disagreeable, bitter, resinous taste, and bear the popular name of "Fel de terra", or earth-gall, are employed by quacks against jaundice, and a belief also prevails that by secretly eating the blossoms youths are enabled to win the affection of the maidens they admire. The same may be said of *Lophophytum Leandri*, and, in addition, there is a tradition that the eating of it brings luck and agility in hunting, fishing, fighting, and dancing, and for this reason the Indian youth collect the plants secretly and eat them on particular days.

Of the other parasitic Balanophoreæ most nearly allied to *Lophophytum* we will here only mention in passing the species of *Ombrophytum*, known in Peru by the name of "Mays del monte", which has a yellowish inflorescence over 30 cm. high, and from 6 to 7 cm. thick, somewhat resembling a spike of maize, and lastly, the *Lathrophytum Peckoltii* of Brazil, to which a special interest attaches inasmuch as it is the sole instance of a flowering plant entirely destitute of all structures of the nature of leaves, with the exception of the stamens and ovaries. *Langsdorfia*, *Scybalium*, *Lophophytum*, and even *Balanophora*, *Helosis*, and *Rhopalocnemis* exhibit scales, which, though transformed in various ways, are yet always in point of position and form recognizable as leaves; but neither on the tuber, shaft, nor spadix of this *Lathrophytum* is any trace of a scale to be seen, nor even a swelling or rim that might be looked upon as a degenerate leaf.

In comparison with equatorial America with its wealth of parasitic Balanophoreæ the corresponding zone of Africa must be called poor so far as these plants are concerned. Possibly further explorations may bring to light a few more of these wonderful vegetable parasites, but it is hardly to be expected that such a variety as is presented in Brazil, the Peruvian Andes, New Granada, and Bolivia will be found. Only three Balanophoreæ have been discovered in the Cape regions, where the flora is well known. One of these, which is represented on the right-hand side of fig. 41, bears the name of *Sarcophyte sanguinea* (i.e. blood-red flesh-plant), whilst the name of *Icthyosoma* (i.e. fish-carcase) has also been applied to it because it smells of rotten fish. These names imply that the plant resembles an animal rather than a vegetable organism.. The host-plants adapted to this *Sarcophyte* are various Mimosæ, especially *Acacia caffra*, *Acacia capensis*, &c. In the first place, as is the case with all Balanophoreæ, small tubers are formed on the roots of the above-mentioned woody hosts, and enter into connection with the wood of the nutrient roots in the manner already described more than once. An inflorescence then emerges from a bud originating beneath the cortex of the tuber, and rapidly grows up from out of the cortex, which is rent and pushed up in the process. The axis of this inflorescence resolves itself into a number of thick, repeatedly ramifying, fleshy branches, differing in this respect from every other

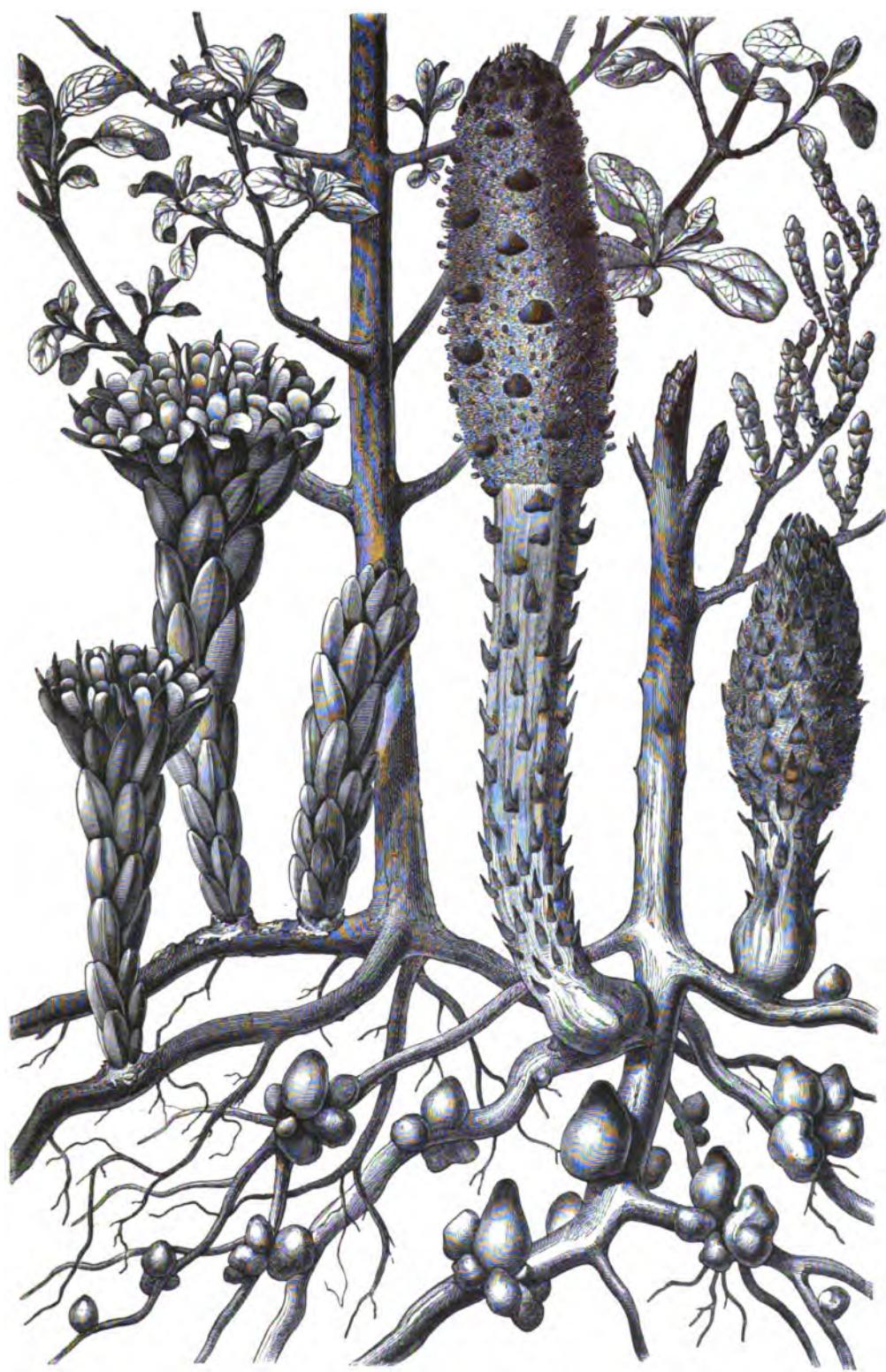


Fig. 42.—*Cytinus Hypocistus* on the left; *Cynomorium coccineum* on the right.

example of the Balanophoreæ. The flowers are arranged side by side on the branches, staminate flowers on one plant, and pistillate flowers on another, the latter always grouped in spherical capitula, as is shown in fig. 41<sup>2</sup>. Reddish-brown scale-like leaves are situated at the points of origin of the branches, and also at the base of the entire inflorescence. The general aspect is that of a bunch of verrucose grapes ascending from the root, or of the fruiting axis of *Ricinus*, and is very striking owing to the blood-red colouring of all the parts.

As a final instance of the Balanophoreæ we may take the genus *Cynomorium*, which was so highly valued in olden times, and is the sole species belonging to this family of plants indigenous in the south of Europe. A drawing of it is given on the right-hand side of fig. 42.

Whilst other Balanophoreæ are parasitic on the roots of trees and lianes in the shade of lofty woods, this *Cynomorium* thrives most luxuriantly upon plants near the sea-coast, on the roots of Pistacias and Myrtles, and even on actual salt-loving maritime plants, the various Tamarisks, Salicorniæ, Salsolaceæ, and Oraches, which are sprinkled with foam whenever the breakers are high. The seed is like that of other Balanophoreæ and those of the Orobanche species, and germinates in the same way as they do. From the group of cells in the seed which represent the embryo, a filiform body emerges, and then grows downwards, its upper part remaining for some time in connection with the other cells in the seed, which are richly furnished with food-materials. The filiform embryo continues to grow deeper and deeper at the expense of this nutritive store, and as soon as it reaches a living root, swells into an oval or irregularly-lobed tubercle, which unites with the wood of the nutrient root in the manner already described. These tubercles swell, and from the summit of each a spadix is produced, as in *Lophophytum*, which is raised above the surface of the earth. The spadix is clothed with pointed scales, and is clearly differentiated into a lower stalk-like support, and a fleshy inflorescence resembling a cone. The small scales are separated from one another by the process of elongation of the spadix, and some fall off. Others of them, situated about the middle of the inflorescence, persist, however, until the time when the entire spadix dries up. The whole of the structure standing above the ground has a blood-red colour, and when it is injured a red fluid exudes, which was at one time supposed to be blood. At an age when the peculiar properties of extraordinary plants were looked upon as an indication given by higher powers that they were to be used for curative purposes, it was believed that the spadices of *Cynomorium*, being blood-red in colour, and bleeding when wounded, had styptic properties. In those days they were even collected for the sake of this property, and sold in apothecaries' shops under the name of the Maltese fungus (*Fungus melitensis*). Various miraculous virtues were also attributed to this plant, and the demand for it was so great that it became a regular article of commerce, its main source being the Island of Malta, whence is derived the name above referred to.

Of the Hydnoreæ, which are most properly included in the same series as

Balanophoreæ in consideration of their coalescence with the roots of their hosts, only three species are known. Two of them (*Hydnora Africana* and *H. triceps*) belong to South Africa, the third (*Hydnora Americana* = *Prosopanche Burmeisteri*) to South Brazil. The tuber is represented by a prismatic body with from four to six angles furnished with papillæ along the edges. The flower-buds which burst from it have at first the form of spherical Gasteromycetes, but gradually elongate and assume the form of a large fig or upright club. This structure opens at the thickened upper extremity by three stout fleshy valves representing petals. At the base of this curious flower no appendage is to be seen that could be interpreted as a bract or leaf. The fleshy mass of flowers evolves a disagreeable putrid odour, and in this property the Hydnoreæ resemble the Rafflesiaæ, which belong to the next group of parasitic Phanerogams.

The fifth series of flowering parasites is composed of the Rafflesiaæ, plants connected with Balanophoreæ and Hydnoreæ by their general aspect, the absence of chlorophyll, and the undifferentiated embryo which consists merely of a group of cells. They used all to be classed together under the name of Rhizantheæ; but the Rafflesiaæ are now treated as a separate family on account of the characteristic structure of their flowers and fruit. The formation of these organs will again come up for discussion later on when we treat of the wonderful structure of the famous giant-flower *Rafflesia*; at present we are only concerned with the relationship of the parasite to the food-providing host-plant. This is, if possible, even more remarkable than in the case of Balanophoreæ and Hydnoreæ. In the latter the union is effected within a structure like a tuber or a rhizome, the vessels and cells of the parasite coalescing with the exfoliated and disordered wood-cells belonging to the root or stem of the host-plant; whereas in Rafflesiaæ the embryo, having penetrated beneath the cortex of the host, produces a more or less definite hollow cylinder which surrounds the wood of the host's root or stem (as the case may be), and constitutes a sort of vestment intercalated between the wood and the cortex of the host. There is no production of tuberous enlargements as in the Balanophoreæ. The stem or root attacked by the parasite only exhibits a moderate thickening at the place where the parasite dwells beneath the cortex, and the cortex itself is only destroyed at the spot where the embryo pierces through it, and where subsequently the flowers emerge. When roots constitute the substratum whereupon the parasite has established itself, they are always of a kind that run throughout upon the surface of the ground; when stems are chosen for attack, they are either the branches of trees or shrubs, shoots clothed with dead foliage belonging to dwarf suffruticose bushes, or else woody lianes of tropical forests. The seeds are conveyed to the host-plants through the intervention of animals.

Rafflesias are found in the haunts of elephants and along the tracks followed by those beasts. The Rafflesia-fruits are accordingly no doubt trampled upon and crushed, and the little seeds imbedded in the pulpy mass of the fruit thus have an opportunity of adhering to the elephants' feet. The seeds are afterwards rubbed off by projecting roots at places more or less remote from the original locality, and if

the root upon which they are detained belongs to a *Cissus* plant, they germinate. On the other hand, such Rafflesiaceæ as occur on the woody branches of trees, shrubs, and undergrowths, or on lianes, develop succulent fruits, which are eaten by animals. Their seeds are protected by a horny coat, and preserve their power of germination unimpaired as they pass through the animals' alimentary canals and are deposited with the excrements on the stems of fresh host-plants; or the seeds may stick to some part of an animal that happens to rub against them, and be brushed off later on as being an uncomfortable appendage, and in this way also they may fall upon the stem of a host-plant. Those Rafflesiaceæ which occur in Venezuela on the woody lianes (*Caulotretus*), known by the name of "monkey-ladders", owe their dispersion for the most part probably to monkeys.

Now, if a seed has been deposited in one way or another upon a woody root, creeping along the surface of the ground, or upon the stem of a woody plant, the filiform embryo emerging from the seed finds a suitable nutrient substratum present and it pierces the cortex of the root, and develops beneath it a tissue, which incloses the wood like a sheath. In *Rafflesia* and in the *Pilostyles* parasitic on the suffruticose shrubs of *Tragacanth* (*P. Haussknechtii*, see fig. 43<sup>1</sup>), this tissue consists of rows of cells, which to the naked eye look like threads. Some are simple and greatly elongated, others branched, and they are united together to form a net-work, so closely resembling the mycelium of a fungus as to be readily mistaken for one. The most complete similarity to these vegetative bodies living beneath the cortex of a host-plant is exhibited by the mycelia of the toad-stools which spread themselves in the form of nets and webs between the wood and the cortex of old trunks of trees. The vegetative bodies of the other species of *Pilostyles* consist, in each case, of a tissue composed of many layers of cells forming a parenchyma imbedded between wood and cortex in the host-plant and including some vessels and rows of cells capable of being interpreted as vascular bundles. Only in rare instances does this tissue of the parasite form an unbroken hollow cylinder encompassing the wood of the host; usually the elements of the host's tissues penetrate into it and permeate and split up the cylindrical soma (vegetative body) in the form of bands, ribs, and fibres. Many elements of the tissues, which the imbedded parasite has displaced from the living wood, and carries, as it were, on its back, perish; but sometimes these discarded layers remain in connection with other living tissues and so preserve their own vitality and power of expansion, and develop layers of wood-cells covering the parasite. There is then a general confusion and entanglement, and it is difficult to say what part belongs to the parasite and what to the host.

When the somatic tissue of the parasite has accomplished its connections with the host-plant in the manner just described, the latter is unable to rid itself of its occupant. A portion of the juices of the host-plant passes into the parasite's cells and the unwelcome guest augments in volume, and endeavours forthwith to reproduce and distribute its kind by the formation of fruit and seeds. For this purpose buds are developed at suitable spots in the reticular body of the parasite, each of which is manifested as a parenchyma of pulvinate appearance, and is

termed a floral cushion. The cells in this cushion, however, now group themselves in a definite way; ducts and vessels are produced, and, at the same time, a differentiation into axis and flowers is exhibited. These members continue their development, increase in size, and finally the enlarged bud breaks through the cortex of the host-plant under shelter of which it has been evolved.

In the genus *Cytinus* alone do we find a stem richly furnished with leaves and bearing at the top a flattened symmetrical tuft of flowers (see fig. 42, left-hand side) developed from this bud; in the rest of the Rafflesiaceæ, the bud, which has

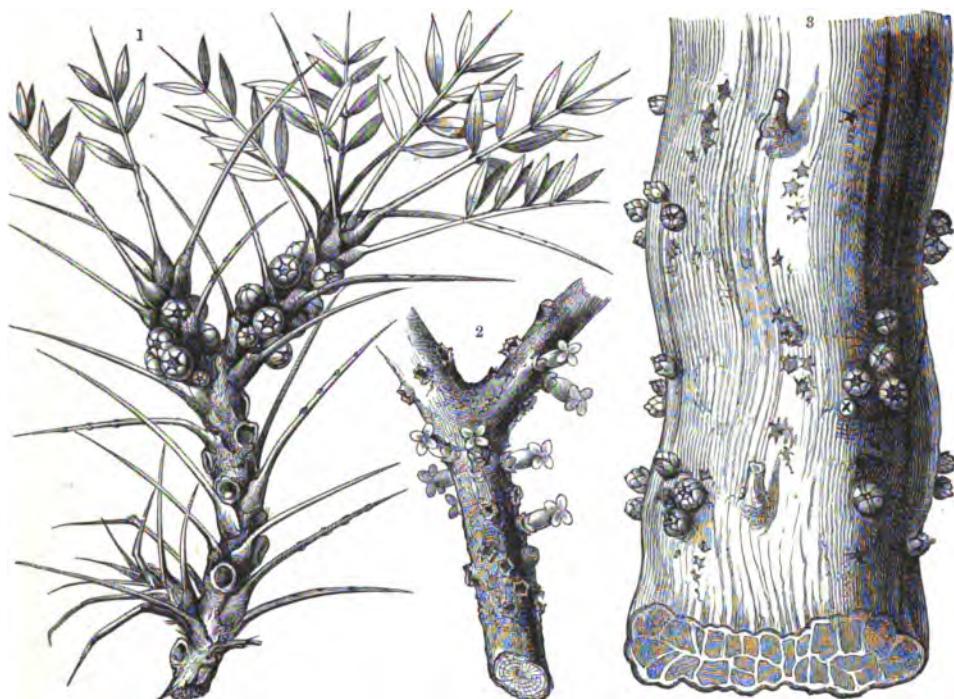


Fig. 48.—Rafflesiaceæ parasitic on trunks and branches.

<sup>1</sup> *Pilostyles Haussknechtii*.

<sup>2</sup> *Apodanthes Flacourtiana*.

<sup>3</sup> *Pilostyles Caulotreti*.

emerged from beneath the cortex of the host, is the flower-bud itself. The axis supporting the bud is extremely abbreviated and clothed merely by a few scales, and the flowers are sessile directly upon the root or stem of the host (see fig. 43). In the case of roots creeping upon the ground, the buds always emerge only on the side turned towards the light; on lianes, also, they are only formed on the side more exposed to light where subsequently the opened flowers are easily accessible to flying insects (see fig. 43<sup>3</sup>); on upright shrubs and under-shrubs, on the other hand, they burst forth on all sides upon the branches. Branches of this kind bearing ubiquitously extruded flowers of a parasite such as *Apodanthes Flacourtiana* (see fig. 43<sup>2</sup>) look delusively like the Mezereon (*Daphne Mezereum*) when the latter is in bloom in the early spring before the development of foliage-leaves, its woody branches being similarly studded all round with flowers, which stand out horizontally

from them; but, in the one case the flowers belong to a foreign parasite living under the cortex and have broken through it, whereas in Mezereon it is the flowers of the plant itself that have unfolded. In the case of *Pilostyles Haussknechtii*, which is parasitic on the low bushy tragacanth shrubs of the Persian plateaus, the buds are formed regularly on both sides of the leaf-bases of the host, so that at the insertion of every one of the older foliage-leaves, one finds a pair of buds, which subsequently expand into flowers (see fig. 43<sup>1</sup>).

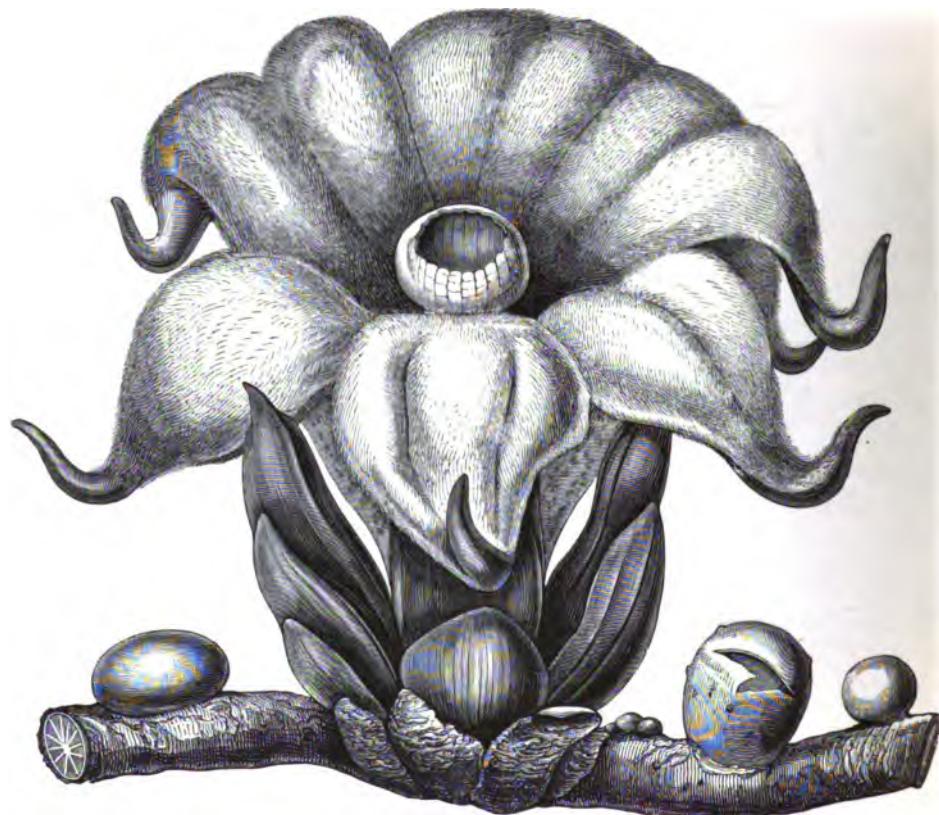


Fig. 44.—Parasitic Rafflesiaceæ (*Brugmansia Zipellii*) upon a *Cissus*-root.

Throughout the species of *Apodanthes* and *Pilostyles* the flowers are small—about the size of elder, jasmine, or winter-green blossoms—and by no means conspicuous. But this is not the case in the genera *Brugmansia* and *Rafflesia*. The *Brugmansias*, indigenous to Borneo and Java, have very handsome flowers, as may be seen in the above drawing, which represents on the natural scale *Brugmansia Zipellii* parasitic upon the root of a *Cissus*. But in magnitude they are far surpassed by the flowers of the *Rafflesiae*, one of which, viz.: *Rafflesia Arnoldii*, may be described as actually the largest flower in the world. When open it has a diameter of 1 meter, a dimension exceeding even that of the gigantic blooms of South American aristolochias. At the period of emergence of the buds of *Rafflesia Arnoldii* from the roots of the vines which serve them as hosts, they

are only as large as a walnut and give scarcely any indication of their future magnitude; but they gradually increase in size, and before opening are curiously like a cabbage. Up to this time the bracts still inclose the flower proper, and to them is due the above-mentioned resemblance. They now open back, and the flower, which, to the last, grows rapidly, unfolds and displays five immense lobes around a central bowl or cup-shaped portion. The form of the giant-flower when open is best likened to that of a forget-me-not blossom. The semicircular outline of the lobes, at least, is similar, and the very short throat of the flower also exhibits a distant resemblance. At the part where the bowl-shaped centre, which



Fig. 45.—*Rafflesia Padma*, parasitic on roots upon the surface of the ground.

has the stamens and styles inserted in it, passes into the lobes there is a thick, fleshy ring like a corona. The upper surface of the lobes is covered with numbers of papillæ. The lobes themselves, the hollow central bowl, and the ring, are all fleshy, and the flower, as a whole, emits an unpleasant putrescent smell. This floral prodigy was first discovered in the year 1818 in the interior of Sumatra at Pulo Lebbas on the river Manna, where it occurs parasitic on the roots of wild vines in places where the ground is strewn with the dung of elephants. It has never yet been seen anywhere outside Sumatra. Four other Rafflesiae have, however, been discovered, but all in the islands of the Indian Ocean—Java, Borneo, and the Philippines. In mode of growth, as also in the form of the flowers, they resemble the species above described, but their flowers are rather smaller. *Rafflesia Padma*, which occurs in Java, and is represented in fig. 45, possesses flowers with a diameter of half a meter. The hollow, somewhat ventricose centre and the ring bordering the floral receptacle are in this *Rafflesia* of a dirty

blood-red, whilst the verrucose lobes have almost the colour of the human skin. The flowers are sessile upon roots which wind about upon the dark forest ground, and a cadaverous smell, anything but pleasant, issues from them. All these peculiarities explain the uncanny impression made by the organisms in question upon their original discoverers and upon all subsequent observers.

Whilst the *Rafflesia*, as well as the genera *Brugmansia* and *Sapria*, belong to the tropical and sub-tropical regions of Asia, and to the world of islands adjacent thereto on the south side, the genus *Apodanthes* is confined to tropical America. Most of the species of *Pilostyles* also appertain to tropical America, especially to Brazil, Chili, Venezuela, and New Granada. One species alone—*Pilostyles Ethiopica*—has been observed in the mountains of Angola, and another, as has been mentioned before, in Persia.

The only European representative of the remarkable group of *Rafflesiaceæ* is *Cytinus Hypocistus*, represented on the left side of fig. 42, but its distribution is coincident with the entire range of the Mediterranean flora. The roots of cistus shrubs, plants which are characteristic of the vegetation belonging to the basin of the Mediterranean, constitute the nutrient substratum in the case of *Cytinus*. It is especially where the layer of earth-mould is not deep, and consequently the roots of the shrubs in question are exposed, that *Cytinus* is met with growing in abundance amongst the under-wood of the cistus plants. The squamous leaves clothing the stem of this parasite being scarlet, and the plants not solitary but in large numbers, one sees here and there a flaming red colour glowing in the gaps in the cistus-groves, and one is thus from far off made aware of the presence of the parasite. The flowers themselves, which open between the red scale-like bracts, are yellow. The combination of colour thus afforded is a rare phenomenon in the vegetable world, and gives a very strange appearance to the plant. Besides the species of *Cytinus* distributed over the area of the Mediterranean flora, there are two other species in Mexico, and one also at the Cape, which, although not parasitic on *Cistus* shrubs but on other woody plants, especially *Eriocephalus*, yet do not differ from *Cytinus Hypocistus* in floral structure or in mode of connection with their host.

#### MISTLETOES AND LORANTHUSES.

The sixth and last series of parasitic phanerogams includes epiphytes of bushy appearance with much bifurcated branches, green cortex, green leaves, and berries containing large seeds, which germinate whilst resting immediately upon the branches of such trees as are adapted to act as host-plants, and will surrender to the invader a portion of their nutriment. To this series belong a dozen different species of the genus *Henslowia*, belonging to the family of Santalaceæ, and indigenous to the South of Asia—chiefly the East Indian Archipelago—and, in addition, upwards of 300 species included in the family Loranthaceæ. Amongst the latter, the plant that is best known and most widely distributed is the European Mistletoe (*Viscum album*) represented in fig. 46, and as it is also fitted, in

respect of its life-history, to serve as type of the entire series, we will describe it first of all.

As is well known, the Mistletoe is parasitic upon trees, and these may be either Angiosperms or Gymnosperms. Most frequently it establishes itself upon trees the branches of which are coated by a soft sappy cortex—an extremely delicate and tender cork-tissue in particular—as is the case with silver-firs, apple-trees, and poplars. The Mistletoe's favourite tree is certainly the Black Poplar (*Populus nigra*). It flourishes with astonishing luxuriance on the branches of that tree, and wherever there is a small plantation of Black Poplars, the Mistletoe takes up its abode.

Along the shores of the Baltic and by the Danube near Vienna—especially in the celebrated Prater from which fig. 47 is taken, one finds, on many of the Black Poplars, tufts of Mistletoe measuring 4 meters in circumference, and with axes of a thickness of 5 cm. Birds use their most crowded branches, by preference, to nest in. In the forests of Karst, in Carniola, and in the Black Forest, where poplar trees play merely a subordinate part, whilst on the other hand, quantities of silver firs shade the ground, large numbers of these conifers have their tops covered with Mistletoe; and in the Rhine districts and the valley of the Inn in Tyrol, the same parasite occurs as a troublesome visitor upon apple-trees in the neighbourhood of the peasants' farms. In localities destitute of these three kinds of trees, which are pre-eminently the Mistletoe's favourite host-plants, it puts up with other trees, and is then usually found on whatever species happens to be the most common in each particular country. Thus, in the Black Pine district of the Wiener Wald, it occurs upon the Corsican Pine, whilst on the heaths of the sandy lowlands of the March, it settles upon the Scotch Pine. Much less frequently it has been observed on walnut-trees, limes, elms, robinias, willows, ashes, white-thorns, pear-trees, medlars, damsons, almond-trees, and on the various species of *Sorbus*. Mistletoe has also been found by way of exception upon the oak and the maple, and upon old vines. On one occasion, in the district of Verona, it has been seen established upon the parasitic shrubs of *Loranthus Europaeus*, that is to say, one member of the Loranthaceæ was found parasitic upon another. The birch, the beech, and the plane, are avoided by the Mistletoe, a fact which no doubt depends upon the special structure of the cortex in those trees.

The dissemination of the European Mistletoe is effected, as in all the other Loranthaceæ, through the agency of birds—thrushes in particular—which feed upon the berries and deposit the undigested seeds with their excrement upon the branches of trees. That a preliminary passage through the alimentary canal of birds is essential to the germination of these seeds is no doubt a delusion, this assumption of former times being easily refuted by the fact that one can readily induce the seeds of berries, taken fresh from a tree, and stuck into fissures in the bark of moderately suitable trees, to germinate; it is, however, true, that in nature, mistletoe-seeds are dispersed exclusively by birds in the manner above mentioned. To this method of dissemination must be attributed the phenomenon, which, at first

sight, is surprising, that Mistletoe-plants are rarely seated upon the upper surface of branches, but very frequently on the sides. For the dung of thrushes, which live upon Mistletoe-berries, is in the form of a semi-fluid, highly viscid mass, ductile like bird-lime; and, even when it is deposited upon the upper surface of slanting branches, it immediately runs down the sides, sometimes extending in ropes 20 or 30 centimeters in length. Owing to the viscous mass thus following the law of gravity, the Mistletoe-seeds imbedded in it are conveyed to the sides, and even to the under surface of the bark, and there remain cemented.



Fig. 46.—The European Mistletoe (*Viscum album*).

It may be a long time before a seed of the kind germinates, especially if it does not become attached until the autumn. The embryo is completely surrounded in the seed by reserve food. It is club-shaped and comparatively large, and is distinguished by the fact that the two oblong cotyledons, which are closely pressed together, but often somewhat wavy at the margins, are coloured dark green by chlorophyll, like the environing cellular mass filled with reserve materials. In the process of germination the axis of the embryo, especially the part lying beneath the cotyledons, and passing into the hemispherical radicle, lengthens out; the white seed-coat is pierced, and the radicle makes its appearance through the breach. Under all circumstances the emergent radicle is directed towards the bark of the branch to which the seed is adherent. This is the case even when the seed chances

to stick with the radicle of the seedling pointing away from the branch; the whole axis of the embryo curving towards the surface of the bark in a very striking manner. Thus the radicle always reaches the bark, and having done so it becomes adpressed and cemented to its surface, spreads itself out in the form of a doughy mass, and so develops into a regular attachment-disc. From its centre a slender process now grows into the bark of the host-plant, piercing the latter and penetrating as far as the wood, but not growing into that tissue. This penetrating process has been termed a "sinker", and must be looked upon as a specially modified root.

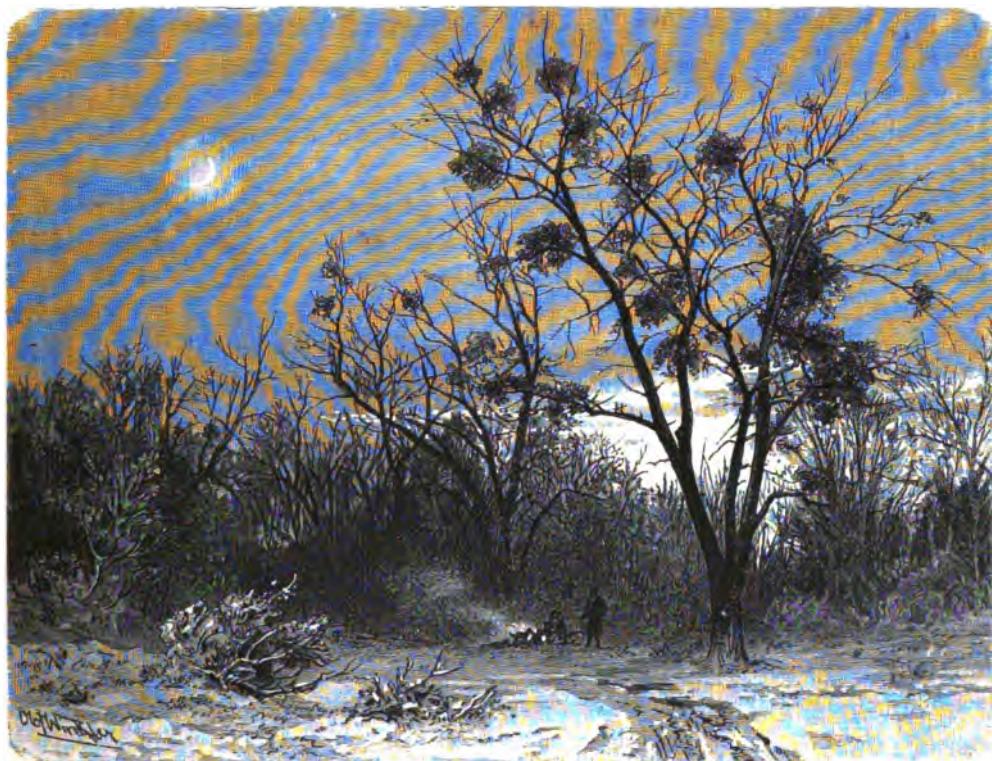


Fig. 47.—Bushes of Mistletoe upon the Black Poplar in winter.

The development of the first year ends with the formation of this sinker. When the winter is over, the branch, into which the sinker is inserted so as just to reach the wood with its point, grows in thickness, a new layer of wood-cells—a so-called annual ring—being superimposed upon the wood of the previous year. The increasing mass of wood first surrounds the tip of the sinker with wood-cells, then forms a rampart all round it, pushing the cortical tissue, wherein that organ has hitherto been wedged, in front of it in an outward direction, and in this way the sinker is at length fixed deep within the woody cylinder. The process of inclosure by the wood-layers, as they are built up, may be compared to the gradual surrounding of a stake on the sea-shore by the rising tide; the lowermost extremity is first immersed and then higher and higher parts until the whole is enveloped. The

sinker itself remains, strictly speaking, stationary; it does not grow into the wood, but the wood overgrows it. But what happens in the following season when a fresh annual ring is once more added to the wood? If the sinker had entirely ceased growing it would of necessity be ultimately completely closed by the layers of wood, as they develop with ever-increasing energy and add to the thickness of the branch, and at last it would be quite buried. To prevent this result, which would be fatal to the Mistletoe, a zone of cells is provided near the base of the sinker, which zone, at the time when the rampart of wood is being raised, adds in an equal degree to its own height, and causes, of course, an elongation of the sinker in a peripheral direction. The length of the piece thus intercalated in the haustorium is exactly equal to the thickness of the corresponding annual ring in the surrounding wood of the branch. Thus at length the Mistletoe-sinker is found imbedded in a number of annual rings, although it has not grown into the latter, but has been banked up by them year by year.

That zone of the sinker which possesses the capacity for growth, and which is always to be sought, in accordance with what has been said above, at the outside limit of the wood of the branch, in the so-called "bast" layer situated on the inner face of the cortex, produces, in the second year after the adhesion of the Mistletoe-embryo, lateral ramifications which are called cortical roots. They are thick, cylindrical, or somewhat compressed filaments, and all run close together under the cortex in the bast layer of the invaded branch. These rootlets issuing from the sinkers pursue a course parallel to the longitudinal axis of the branch, whilst the sinkers themselves are at right angles to the axis (see fig. 48<sup>3</sup>). If a rootlet springs from the sinker in a direction transverse to the longitudinal axis it bends immediately afterwards so as to be parallel to the long axis, and adopts the same direction as the rest, or else it bifurcates just above its place of origin into two branches which separate suddenly, and in their further course follow the axis of the branch. Thus it comes to pass that all the rootlets of a Mistletoe run up and down in the infested branch of the host-plant in the form of thick green parallel strands, but that none of them ever encircle the branch in the form of an annular coil. Each of these cortical roots may now develop from behind the growing-point new sinkers, which are formed in the same way as the first one above described as proceeding from the actual seedling. They, too, penetrate into the branch perpendicularly to the axis, and as far as the solid wood are then encompassed by the growing mass of wood, but maintain the power of growth in the part close to their insertions, and in their growth keep pace with the thickening of the wood of the branch. The fact of the yearly recurrence of this formation of sinkers explains how it is that those situated nearest the growing-points of the cortical roots are the shortest, they being the youngest, whilst those which arise near the first sinker are the longest and oldest. It also accounts for the former being only inclosed by one annual ring of the host's wood, and the others being surrounded by an increasing number of rings the nearer they are to the spot where the Mistletoe-plant first struck root.

The root-system of the Mistletoe taken as a whole may be described as like a jaw-bone in shape, or, still better, a rake. The cross-beam of the rake corresponds to the cortical root, whilst the teeth are analogous to the sinkers; the cross-piece must be supposed to be parallel to the axis of the branch and lying under the bark, and the spokes must be thought of as perpendicular to the axis and driven into the wood.

Whilst the roots of the Mistletoe-plant are spreading in the interior of the branch in the manner described, the stem is developed outside. At the time when the process, subsequently to be the first sinker, emerges from the attachment-disc of

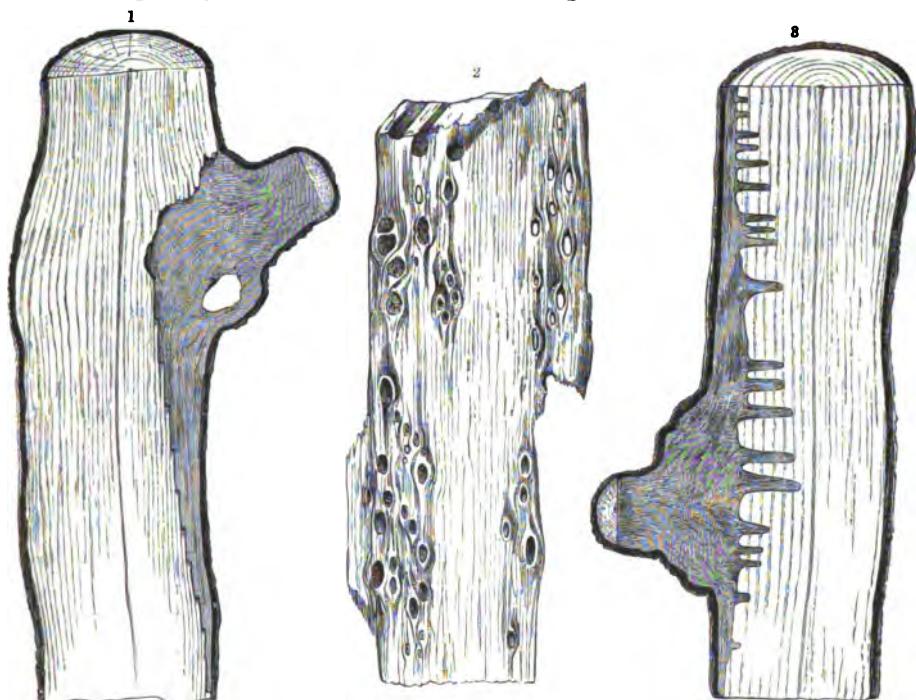


Fig. 48.—<sup>1</sup> *Loranthus Europaeus*, and <sup>2</sup> Mistletoe (*Viscum album*)—both parasitic on branches of trees, and seen in section.  
<sup>3</sup> A piece of the wood of a Fir-tree perforated by the sinkers of a Mistletoe.

the embryo and pierces through the bark, the cotyledons are still covered by the white seed-coat, which rests upon them like a cap. But when once this first sinker is firmly fixed and in a position to take up nutritive juices from the wood of the host, the seed-coat is thrown off; the apex of the stem, which is still very short, is raised; the cotyledons are detached, whilst close above them is produced a pair of green leaves. Thenceforward the development of the visible portion of the Mistletoe-plant outside the bark keeps pace with that of the roots underneath the cortex, and is moreover dependent upon the quantity of food taken up by the sinkers from the wood. Where there is an abundant supply of nutriment, as in the case of poplars, the growth of the Mistletoe is correspondingly exuberant; where the flow of juices is scarce, the parasite is stunted in its growth, and often develops only small yellowish sickly-looking tufts. If the foster-plant is of a lavish nature, adven-

titious buds are produced regularly by the cortical roots to which the absorbed nutriment is first of all conveyed from the sinkers. These buds occur on the side of the rootlets nearest the exterior of the bark, and later they burst through the rind, and develop into new Mistletoe-plants.

These outgrowths are analogous to the adventitious shoots produced from the subterranean roots of the Aspen, and this comparison is rendered all the more appropriate by the fact that the removal of the tuft of Mistletoe encourages the sprouting of adventitious root-buds just as in the case of the Aspen, the growth of shoots from the roots is promoted by the felling of the trees to which those roots belong. If a large Mistletoe-bush, growing in solitude on a Black Poplar, is removed from the tree with the intention of freeing the latter from its parasite, the hopes entertained by the operator are disappointed; for, an outgrowth of shoots from the cortical roots ensues at a number of different spots, and in a few years' time the poplar in question is the prey of a dozen Mistletoe-bushes instead of one. Inasmuch as these bushes, produced from offshoots, are able, under favourable conditions, to send out fresh roots, and these again may develop shoots, a good host of the kind will at last have all its boughs from top to bottom overgrown by Mistletoes. In the Prater at Vienna there are poplars beset by at least thirty large Mistletoe-shrubs, and double that number of small ones, and if one catches sight of such a tree at some distance in winter-time when the branches have lost their leaves, one takes it to be a Mistletoe-tree, for almost the entire system of branches is mantled in a continuous tangle of evergreen bushes of Mistletoe, which are in a state of parasitism upon it.

Sinkers of the Mistletoe, 10 cm. in length, and inclosed in forty annual rings, have been found in the wood of the Silver Fir, whence we may conclude that the Mistletoe may live for forty years. A greater age could scarcely be attained by one and the same bush of the parasite. If the Mistletoe dies, the rootlets and haustoria survive for a time, but at length moulder and fall to pieces, whilst the wood in which they were imbedded remains unaltered. The affected parts of the wood exhibit in that case numerous perforations, and look just like the wood of a target which has been fired at and struck by shot or small bullets (see fig. 48<sup>2</sup>).

A small plant belonging to the Loranthaceæ and named Juniper-Mistletoe (*Viscum Oxycedri* or *Arceuthobium Oxycedri*) occurs on the red-berried juniper bushes (*Juniper Oxycedrus*) of the Mediterranean flora. It is very different from the common European Mistletoe, as is obvious at first sight, its foliage-leaves being reduced to little scales, which gives a characteristic jointed appearance to the ramifications. A whole series of leafless forms allied to this species is found to exist in India, Japan, Java, Bourbon, Mexico, Brazil, and at the Cape. They are nearly all small bushes which project from the boughs of host-plants and sometimes clothe the latter so thickly that the boughs in question serving as nutrient substratum are entirely enshrouded by the parasitic growth. The Juniper-Mistletoe is only from 3 cm. to 5 cm. tall, and the branchlets are not woody, but soft and herbaceous; the fruits are blue oblong berries, almost destitute of succulence. The latter are

dispersed by birds like the berries of the common Mistletoe, and the way in which the parasite settles upon and clings to branches of the host-plant is the same as in that species. It also develops sinkers and cortical roots, but these root-structures are not by any means so regularly arranged as in *Viscum album*, but form an inextricable web of strands and filaments pervading the internal layers of cortex, and resolving itself into finer and finer groups of cells, which end by looking not unlike a mycelium, and also remind one of the suction-apparatus possessed by Rafflesiaceæ. Such of these strands and cellular filaments as are imbedded in the wood of the juniper do undoubtedly play the part of suction-organs. They are present in large numbers, and some of them are occasionally encompassed by several annual rings. They possess no special zone of growth. The elongation necessary to prevent their being enveloped and overwhelmed by the wood, as it adds to its thickness, is effected by the division of individual cells and groups of cells. The outgrowth of shoots from the root is much more exuberant than in the common Mistletoe; but the death of the original plant takes place much earlier, and close to yellowish-green bushes of various degrees of smallness, one finds very regularly dead or dying shrublets already turned brown, all growing promiscuously over the somewhat swollen branches of the red-berried Juniper.

The behaviour of *Loranthus Europæus*, which is parasitic on oaks and chestnuts in the east and south of Europe, is altogether unique. The mode of its attack upon the branches of oaks is, it is true, similar to that of the two other Loranthaceæ just described. The yellow berries, which are grouped in graceful biseriate racemes, are eaten with avidity by thrushes in the autumn and winter, and the undigested seeds are deposited with the dung of those birds upon the branches of trees. The embryo, on emerging from the seed, bends towards the bark and sticks to it, at the bottom of little rifts and crevices, for the most part, by means of the radicle, which becomes an attachment-disc. A process grows in the next place from the centre of the attachment-disc, and pierces through all cortical layers of the oak-branch as far as the interior of the young wood, as if it were a small nail driven in. This process increases in thickness at the expense of the nutriment it withdraws from the young wood, and from it are developed one, two, or three branches, which, however, invariably run downwards beneath the bark, that is to say, in the direction opposed to that of the stream of sap ascending in the oak-wood, and never produce the sinkers so characteristic of the Mistletoe. Each of these roots is shaped like a wedge, even from the rudimentary stage, and acts, too, in the manner of a wedge, penetrating between the yet soft and delicate cells of the cambium, which were formed in the spring at the periphery of the solid older wood of the previous year, and were destined to constitute a new annual ring, splitting and tearing in the process that cell-tissue. Such of these tender cells as lie outside the wedge die, those situated within become lignified and altered into solid wood, to which the wedge-shaped root firmly adheres. Beneath the apex of the wedge, the lignification of cambium cells naturally extends much further towards the exterior, because there it is not at all broken or dead. In front of the apex of the wedge, therefore, there

is, presently, solid resisting wood. The root being no longer able to split the tissue with its point, is stopped in its growth at this spot. But there is nothing to prevent its continuing to grow along a course somewhat nearer the periphery, and outside the limit of the new annual ring of solid wood, where a fresh development of soft and tender cells has taken place in the cambium, and this indeed actually happens.

Thus, every addition to the length of the *Loranthus*-root, as it grows onward between the wood and the cortex of the oak-branch, is further removed from the axis of the branch; or, in other words, the surface of contact between root and wood has the conformation of a flight of stairs, of which the lowest step constitutes the base, and the uppermost the apex of the root (see fig. 48<sup>1</sup>). These steps are very small, their height varying from about 5 mm. to 7 mm., but they may be distinguished quite clearly in longitudinal sections, on account of the darker colour of these roots contrasting with the lighter oak-wood. Nutritive fluids are imbibed by the *Loranthus*-root from the wood of the oak at the surface of contact, and it is probable that this absorption takes place especially at the notches forming the steps. The root can only elongate, naturally, during the period when there is a young and fragile cell-layer superimposed upon the solid wood, whence it follows that in *Loranthus* the continuation of the root's growth is more dependent upon a particular season and upon the annual progress of development of the host than is the case with the Mistletoe. There may be some connection between this circumstance and the fact that the Mistletoe possesses evergreen leaves, whilst *Loranthus* is green only in summer, acquiring fresh green foliage in the spring in the very same week as the oak does, and casting its leaves in the autumn simultaneously with the tree it infests.

The stem which issues from the embryo of a *Loranthus*-seed grows away from the oak-branch into the open air, and develops with great rapidity at the expense of the nutriment absorbed from the host's wood, and conveyed to it by the root above described, into a dense, dichotomously-branched bush. In summer it is not unlike a Mistletoe-bush, but in autumn, when it has cast its leaves, it acquires a totally different aspect owing to the dark-brown branches and the conspicuous yellow clusters of berries.

Bushes of *Loranthus* grow to a greater size even than those of the Mistletoe; their stems attain not infrequently a thickness of 4 cm., and clothe themselves with a blackish, rugged bark, the older stems of this kind being then usually studded by an abundance of lichens. At the spots where stems of *Loranthus* spring from an oak-branch they are always surrounded by a great rampart of wood belonging to the oak, and the base of the stem is often fixed in a deep symmetrically-rounded bowl reminding one vividly of the similar structures out of which the stems of *Balanophoreæ* arise. But whereas in *Balanophoreæ* this bowl-shaped rampart appertains to the parasite, in *Loranthus* it is formed from the wood of the host-plant, i.e. the oak. It must, in the case we are considering, be interpreted as an exuberant growth of wood-cells and compared to the hypertrophies called galls,

which will be treated of in detail in a subsequent part of this book. On old oaks in the east of Europe these growths round the bases of *Loranthus*-plants sometimes reach the size of a man's head. In the case of a bush of *Loranthus* nearly 100 years old, from the Ernstbrunner Wald, in Lower Austria, which had reached a height of 1·2 m. and a circumference of 5·5 m., the hypertrophy in question measured 70 cm. round. It is not only the base of a bush that is overgrown by wood-cells, but the older portions of the roots described above are frequently walled in and partially inclosed by the wood of the branch as it becomes thicker. They may often be seen fixed deep in the wood, yet still preserving their freshness and vitality, and this is to be explained by the fact that they retain connection with other parts of the roots by means of isolated ledges and bridges. Indeed an adventitious shoot may develop from a piece of a root thus deeply wedged in the wood of the oak, and this shoot then grows so outwards and breaks through all the layers lying above it and originates a young bush, which pushes roots under the host's bark and afterwards behaves in exactly the same manner as a plant produced from a seed cemented to the oak-branch.

The *Loranthus* chosen here for description (*L. Europaeus*) has only small inconspicuous yellowish flowers; on the other hand, under the tropical sun of Africa, Asia, and, above all, Central America, the parasitic species of this genus are amongst the most splendid-flowered of plants. There are species in the tropics—e.g. *Loranthus formosus*, *L. grandiflorus*, and *L. Mutisii*—whose flowers attain a diameter of 10, 15, or even 20 centimeters, and are besides clothed in the most gorgeous purple and orange colours. Many *Loranthi* are like small trees grafted upon other trees. The host-plants of these *Loranthi* are principally angiospermous trees; members of the genus have also repeatedly been met with parasitic upon one another—as, for instance, *Loranthus buxifolius* upon *L. tetrandrus* in Chili. The fact has been already mentioned that the European Mistletoe has been observed near Verona parasitic upon *Loranthus*. It is also worth noticing, in order to complete the account of the complex relationships between parasites, that one species of *Viscum* has been found in India parasitic upon another, viz.:—*Viscum moniliforme* on *V. orientale*.

## GRAFTING AND BUDDING.

Parasitism of one woody plant upon another, such as occurs in the case of *Loranthaceæ*, calls to mind certain modes of organic union between woody plants that are artificially effected by gardeners. From ancient times gardeners have performed special operations which are known as processes of "ennobling", and consist in the transference of the branch or bud of one plant on to another plant as substratum, and the inducement of organic union between the two. The plant from which the branch or bud is taken is perhaps a valuable variety of fruit-tree, or a handsome specimen of an ornamental shrub, whilst for the purpose of a substratum a robustly-growing individual belonging to a wild species of shrub or tree is selected

as a rule, and constitutes the so-called wild "stock". The branch which yields the bud for the operation or which is itself transferred in its entirety to the wild stock is named, in the terminology of horticulture, the noble "scion".

The process of ennobling is effected either by grafting or by budding. In grafting the stem of the stock is cut off transversely, an excision is made at the periphery of the surface of the section and the scion is inserted in this opening. The scion must be previously trimmed to fit; in preparing it care must be taken that it bears a pair of healthy buds, and that the end to be inserted is cut so as to correspond to the form of the fissure made in the stock. In inserting it one must see that, as far as possible, the bark, bast, and wood of the one come into contact with the corresponding parts of the other. The wounds of the stock caused by the operation are then covered by a mass of putty, wax, or some other protective medium, and the chances are that the branch thus introduced will contract an organic union with the substratum, that nutritive matter will be supplied it by the substratum, and that new branches will sprout from its buds. In this case therefore the nutriment taken from the ground by the stock passes into the grafted scion, and the scion, which develops branches from its buds, and ultimately may become a densely ramifying tree-top, behaves as a parasite, whilst the stock plays the part of host.

It not infrequently happens that a substratum supporting at its summit the branches of a grafted scion develops subsequently branches of its own lower down as well, and the curious sight is then afforded of a tree or shrub bearing different foliage, flowers, and fruit on its inferior parts from those of its upper regions. If, for example, the stem of a Quince is used as substratum, and Medlar branches are grafted upon it, the result may be a bush or tree which exhibits below branches with the round leaves, rose-coloured flowers, and golden "pomes" of the Quince, and above branches with the oblong leaves, white flowers, and brown fruit of the Medlar. Gardeners, of course, do not willingly allow this to happen, but carefully remove the branches belonging to the stock in order that all the food materials may fall to the lot of the grafted plant, and the latter thrive as vigorously and luxuriantly as possible.

The same result is obtained by budding as by grafting; but here a single bud of the scion, instead of an entire branch, is transferred to the stock. This is accomplished in the following manner:—Two incisions at right angles forming a T, are made in a branch of not too great age belonging to the plant employed as substratum. These cuts are carried through the bark as far as the wood. The two lobes of bark, formed by the T-shaped incision, are then carefully raised from the wood, and the bud to be transplanted is pushed in under them. The bud which has previously been taken away from the scion must have retained in that process a portion of bark, and usually the bit of bark peeled off is given the shape of a little shield. This shield, carrying the bud that is to be transferred upon it, is now introduced between the two lobes above mentioned, and the lobes are folded over it in such a manner as to allow the bud to project freely from the slit between the

lobes. Besides this, the whole is held together by a bandage, the shield in particular with its bud being pressed firmly on to the new substratum, and thereupon, as a rule, coalescence takes place at once, and the inserted bud grows out into a branch which stands in exactly the same relation to the stock as a *Loranthus* to the oak whereon it is parasitic. All the branches belonging to the substratum, that is to say, to the wild stock, may then be removed, leaving only the one branch that has sprung from the stranger-bud, the result being that all the juices absorbed from the ground by the substratum are concentrated in this branch and cause it to grow with the greatest exuberance.

There is between this process of budding and the settling of a parasite a further resemblance in that shrubs and trees cannot all be made to unite at pleasure one with the other. A successful result of grafting or budding can only be counted upon when nearly allied species, belonging to the same genus or family, are employed for the purpose. Almonds, peaches, apricots, and plums can be grafted the one upon the other; so also can quinces, apples, pears, medlars, and white-thorns. But we must relegate to the realms of fiction such assertions as that peaches might be successfully grafted upon willow stocks, or that the Siberian Crab (*Pyrus salicifolia*) has sprung from the grafting of branches of the Pear upon the Willow and other tales of the sort. Whether it is possible by grafting or budding to produce new forms, or at least hybrids, is a question which will claim our attention in connection with the problem of the origin of new species. The only additional remark to be made here is that notwithstanding the undeniable similarity between grafted or budded plants and the parasitic Loranthaceæ, a very essential difference exists in the circumstance that the latter develops roots which continue to grow year by year, and are always penetrating into new layers of the host's tissues, whereas this is never observed in the case of grafted or budded plants. When the branch of a Peach is grafted on an Almond-tree, there is, it is true, an organic union of the two at the place of contact, and the juices from the wood of the Almond stock are conducted direct into the grafted Peach-branch; but neither roots nor sinkers ever arise from the base of the adnate branch or penetrate into the stem of the Almond-tree.

---

### 5. ABSORPTION OF WATER.

Importance of water to the life of a plant—Absorption of water by Lichens and Mosses, and by Epiphytes furnished with aerial roots—Absorption of rain and dew by foliage-leaves—Development of absorptive cells in special cavities and grooves in the leaves.

### IMPORTANCE OF WATER TO THE LIFE OF A PLANT.

In the building up of the molecules of sugar, starch, cellulose, fats, and acids, of proteids, and, in short, of all the important substances of which a plant is composed, atoms of water have to be incorporated as constructive material, and without water no growth or addition to the mass of a plant whatsoever could take place. From this point of view water must be considered just as indispensable an item in the food of plants as the carbon-dioxide of the air. But water plays, in addition, another important part in plant-life. The mineral salts which serve to nourish hydrophytes, land-plants, and lithophytes, as also the organic compounds which are the food of saprophytes and parasites, can only reach the interior of plants in the form of aqueous solutions. They can only pass through a cell-wall when it is saturated with water, and, having reached the interior of a plant, they can only be conveyed to the places where they are worked up through the medium of water. In connection with the discharge of these functions in a living plant, water must be regarded as a dynamic agent. Just as a mill on a stream only works so long as its wheels are kept in motion by the water, and stops at once if the latter fails, or flows by in insufficient quantity, so the living plant, as it nourishes itself, grows and multiplies, needs a continuous and abundant supply of available water to render possible the performance of the complicated vital processes within it. This available or organizing water is not in chemical combination like that which is present as food-material, and is, in general, not permanently retained. On the contrary, we must conceive it as perpetually streaming through the living plant. In the course of a summer, quantities of water, weighing many times as much as the plant itself, pass through it. The total amount of water in chemical combination in the organic compounds of a plant is very trifling compared with this, though it often happens that the weight of the latter in a particular plant is greater than that of all the other substances put together.

Inasmuch as this water evaporates from plants in dry air, and that it may also easily be withdrawn by alcohol or other means, very simple experiments suffice to give an idea of the great bulk of free water in any plant. Berries, fleshy fungi, succulent leaves, and things of that kind, if left in alcohol, are reduced in a short time to barely half their size in the fresh state. The *Nostocineæ*, which are gelatinous when alive, and many fungi (e.g. *Guepinia*, *Phallus*, *Spathularia*, *Dacryomyces*) shrivel us so stringently in drying, that a piece possessing an area of 1 square centimeter when fresh leaves only a dry crumbling mass covering scarcely 3 square millimeters. A *Nostoc*, which weighed 2.224 grms. in the fresh state only

weighed 0·126 grm. after desiccation, so that when alive it must have contained 94 per cent. of water. Bog-moss, weighing 25·067 grms. before the abstraction of the water was reduced to 2·535 grms. afterwards, showing that the percentage of water was 90. Similar results are obtained in the cases of succulent leaves and stems of flowering plants, *Cucurbita*, and other fruits. The least proportion of water is contained by mature seeds, solid stony seed-coats, wood, and bark; but even in these an average proportion of 10 per cent of water has been detected. We shall not go wrong in assuming, on the evidence of the weights determined, that most parts of plants, when fresh, consist of dry substance only as regards a third, and as regards two-thirds, of water of imbibition, which passes over into the surrounding air in the form of vapour when desiccation takes place.

From all this it follows that water is absolutely necessary to plants as food-material, that it is indispensable as a medium of transport of other substances, and that the demand for water on the part of all plants is very great. Further, we may infer that the importation and exportation of water must be regulated with exactitude if the nutrition is not to be disturbed and development hindered.

Water-absorption is at its simplest in hydrophytes. In this case it coincides with the absorption of the rest of the food-materials, and there is therefore nothing material to add to the statements already made on that subject.

As regards land-plants, lithophytes, and epiphytes, we may likewise refer to what has been already said in so far as these plants suck up water at the same time as food-salts, by means of absorption-cells, from the substratum to which they are attached, or the earth in which they are rooted; but to the extent that they take also water direct from the atmosphere, and have the power of absorbing that water immediately they require it, must be discussed in the following pages.

#### ABSORPTION OF WATER BY LICHENS AND MOSSES, AND BY EPIPHYTES FURNISHED WITH AÉRIAL ROOTS.

The plants which absorb water direct from the atmosphere may be classified in several groups with reference to the contrivances adapted to the purpose. Of all plants lichens are most dependent on atmospheric moisture. Many of them, especially the Old Man's Beard Lichens, which hang down from dried branches of trees, and the gelatinous, crustaceous, and fruticose lichens, which cling to dead wood, and on the surface of rocks and blocks of stone, do in fact derive their necessary supply of water entirely from the atmosphere, and that by absorbing it, not in a liquid but in a gaseous form. The latter circumstance is of the greatest importance to those species in particular which occur on receding rocks, or on the under face of overhanging slabs of stone. Rain and dew cannot reach such places directly, but only by some of the water trickling down from the wet top and sides of the rocks on to the receding wall, and this happens but seldom. Accordingly, lichens occurring in situations of the kind are entirely dependent upon the water contained in the air in the form of vapour. Lichens, however, are also, of all plants,

the best adapted for the absorption of aqueous vapour from the air. If living lichens, which have become dry in the air, are left in a place saturated with moisture, they take up 35 per cent of water in two days, and as much as 56 per cent in six days. Water in the liquid form is naturally absorbed much more rapidly still. When Gyrophoras, which project in the form of cups after a long continuance of dry weather, are moistened by a fall of rain, they swell up completely within ten minutes, and spread themselves flat upon the rocks, having in that short space of time absorbed 50 per cent of water. The saying, "Light come, light go," is no doubt true in these cases. When dry weather sets in, evaporation from the masses of lichens goes on at a pace corresponding to the previous absorption. In the Tundra, the lichens, which form a soft tumid carpet when moistened by rain, are liable to be so powerfully desiccated in the course of a few hours of sunshine, that they split and crackle under one's feet, so that every step is accompanied by a crunching noise.

In the power of condensing and absorbing the aqueous vapour of the atmosphere, lichens are most analogous to mosses and liverworts, and to those pre-eminently which live on the bark of dry branches of trees or on surfaces of rock, covering places of the kind with a carpet which is often enough interspersed and interwoven with lichens. Like the latter these mosses and liverworts are able to remain as though dead in a state of desiccation for weeks together, but as soon as rain or dew falls upon them they resume their vitality; and similarly if the air is so damp as to enable them to derive sufficient water of imbibition from that source. A specimen of *Hypnum molluscum*, a moss which covers blocks of limestone in the form of soft sods, was after a few rainless days detached from the dry rock and placed in a chamber saturated with vapour, and it was found that after two days it had absorbed water from the air to the extent of 20 per cent, after six days 38 per cent, and after ten days 44 per cent. Many mosses condense and absorb water with the whole surfaces of their leaflets, others—as, for example, the gray rock-mosses clinging to slate formations (*Rhacomitriæ* and *Grimmiæ*)—do so especially with the long hair-like cells at the apices of the leaflets, whilst others again only use the cells situated on the upper saucer-shaped or canaliculate leaf-surface.

In some bearded mosses (*Barbula aloides*, *B. rigida*, and *B. ambigua*) chains of barrel-shaped cells occur closely packed together upon the upper surface of the leaf and at right angles to it, which to the naked eye have the appearance of a spongy dark-green pad. The terminal cells of these short moniliform chains have their upturned walls strongly thickened, but the other cells have very thin walls and take up water rapidly. It is the same with the various species of *Polytrichum*, which are provided on their upper leaf-surfaces with parallel longitudinal ridges likewise composed of thin-walled, highly-absorbent cells. The rhizoids also play an important part in these processes. These brown, elongated, thin-walled cells entirely clothe the moss stems, usually in the form of a dense felt, and often project from the under surface of the leaves, whilst in a few tropical species they make their appearance, strangely enough, in the form of little tufts at the apices of the

leaflets. In many instances this felt of rhizoids does not come into contact at all with the soil, rock, or bark (as the case may be), but is surrounded by air alone, and is able to condense or attract, to use a common expression, the aqueous vapour of the air like a piece of cloth or blotting-paper. In dry weather, it is true, mosses, like lichens, lose their water, but they part with it much more slowly than the latter. This is chiefly due to the fact that the moss-leaflets at the commencement of a drought wrinkle, curl up, become concave, and lay themselves one above the other, so that the water is retained at the bottom for a longer period.

A very remarkable contrivance for the absorption of water from the atmosphere is also exhibited by the white-leaved Fork-mosses (*Leucobryum*) and Bog-mosses (*Sphagnaceæ*). Although they possess chlorophyll, and assimilate under the

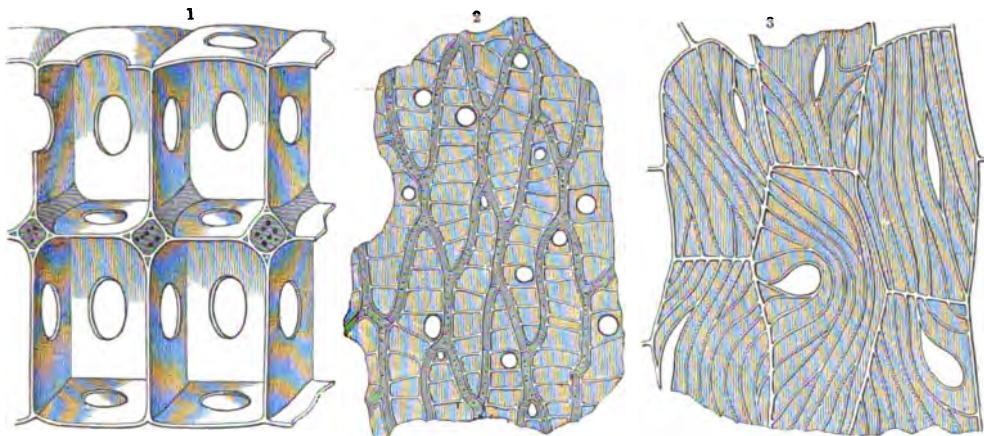


Fig. 49.—Porous Cells.

<sup>1</sup> Of the white-leaved Fork-moss (*Leucobryum*);  $\times 550$ . <sup>2</sup> Of the Bog-moss (*Sphagnum*);  $\times 230$ . <sup>3</sup> Of the root of an Orchid (*Laelia gracilis*);  $\times 310$ .

influence of sunlight, yet they look like parasitic and saprophytic plants destitute of chlorophyll. They are of a whitish colour and always grow in great cushion-like sods, so that the spots where they grow are deficient in verdure, and stand out conspicuously from their surroundings in consequence of their pale tint. Microscopic investigation at once explains this appearance. The cells containing chlorophyll and living active protoplasts are relatively small, and, as it were, wedged and hidden between other cells many times as great, which have entirely lost their protoplasm by the time they are mature, and then cause the paleness of colour appertaining to the plant as a whole. The walls of these large colourless cells are very thin, and in the Bog-mosses have spiral thickening-bands running round them, being thus secured against collapse. After remaining for a time in a dry environment they are full of air only; but the moment they are moistened they fill with water. If there were an actively absorbent protoplast at work in the interior, the water would be able to pass into the cell-cavity through this easily moistened wall, as in the case of other mosses, owing to the delicacy of the cell-membrane. But the air which fills the cells is not absorptive, and in the case of *Leucobryum* and Bog-mosses the water reaches the interior, not in consequence of

a chemical affinity on the part of the cell-contents, but solely by capillary action. All the cell-walls are perforated and furnished with pores, and through these the water rushes into the interior with lightning rapidity.

This extremely rapid influx of water into an air-filled cavity leads us necessarily to the conclusion that each cell has a number of pores in its walls, and that in proportion as water enters through one of the small apertures the air can escape equally fast through another. This is in fact the case. The large cells not only have pores on their external walls, but communicate one with another by similar holes, and the water soaks in from the one side as it does into a bath-sponge, whilst the air is at the same time forced out on the other. This absorptive apparatus is exceptionally elegant in *Leucobryum*, which grows abundantly in many woods. In it, as is shown in the illustration above (fig. 49<sup>1</sup>), the adjacent prismatic cells communicate by highly symmetrical, circular gaps made in the middle of the partition-walls, whilst in the Bog-mosses (the various species of *Sphagnum*), they are to be seen scattered here and there between the thickening bands on the cell-walls (see fig. 49<sup>2</sup>). Now these porous groups of cells possess not only the power of taking up water in the liquid state, but also that of condensing it when in the form of vapour. There is no need of any more proximate proof of the fact that the cells previously mentioned as containing chlorophyll, and lying imbedded between the large perforated cells, take up water supplied by the latter, or perhaps it is better to say that the large perforated cells suck in the water for the living green cells. We have only to ask why it is, then, that these small green cells do not absorb water themselves direct from the environment, as is done in the case of so many other mosses and liverworts. It is difficult to answer this quite satisfactorily, but thus much seems certain, that the large porous cells, when full of air, afford a means of protecting the small living cells from too excessive desiccation, and that they are in addition preservative of the chlorophyll in the small cells, a matter to which we shall return presently.

A certain resemblance to these Leucobryums and Sphagnums, in respect of water-absorption, is exhibited by a few Aroideæ, and more especially by a whole host of Orchidaceæ. Of the 8000 different orchids hitherto discovered, a good proportion, it is true, are rooted in the earth. But more than half these wonderful plants flourish only on the bark of old trees, and most of them would quickly perish if they were detached from that substratum and planted with their roots buried in earth. A double function appertains to the roots of these Orchideæ which inhabit trees. On the one hand they have to fix the entire orchid-plant to the bark, and, on the other, to supply it with nutriment. When the growing tip of an orchid's root comes into contact with a solid body, it adheres closely to it, flattens out more or less, sometimes even becoming strap-shaped (see fig. 15), and develops papilliform or tubular cells, which grow into organic union with the substratum, and might conveniently be termed clamp-cells. In many cases these cells creep over the bark, divide, interlace, and form regular wefts. The organic connection with the substratum is so intimate that an attempt to separate the two usually results

in a detachment of the most superficial parts of the bark, but not of the tubular cells. Now, if a root, after having sent out cells of this kind which contract an organic union with the substratum, reaches into the open, beyond the limit of the



Fig. 50.—Aërial Roots of an Orchid epiphytic upon the bark of the branch of a tree.

substratum, it immediately ceases to develop clamp-cells, loses its ligulate shape, and hangs down from the tree in the form of a sinuous white filament. A few root-fibres are as a rule sufficient to fix the plant to its substratum, the bark of the tree, and the rest of the roots put forth by the orchid grow from beginning to end

freely in the air. They are not infrequently to be seen crowded together in great numbers at the base of the plant, forming regular tassels suspended from the dark bark of the branches as may be seen in fig. 50, where an *Oncidium* is represented.

Each of these aërial roots is invested externally by a white membranous or papery envelope, and it is the cells of this covering that own the resemblance, above referred to, to the cells of *Leucobryum* and Bog-mosses. Their walls are furnished with narrow, projecting spiral thickenings and therefore do not collapse, notwithstanding their delicacy or the circumstance of their inclosing at times an air-filled cavity; they are further abundantly perforated, two kinds of apertures indeed being found. The one variety arises in consequence of the tearing of the portions of the cell-wall situated between the rib-like projections and consisting of extremely thin and delicate membranes (see fig. 49<sup>3</sup>); the existence of the other variety is due to the detachment of the cells which protrude in the form of papillæ, the result being, in this latter case, the formation of circular holes very similar to those already described as occurring in *Leucobryum*. The cells resembling papillæ have the peculiarity that they roll off when they get old in the form of spiral bands. The holes, of course, can only occur on the external walls of the outermost cells which border upon the open air, whilst in the interior the communication between the cells themselves is established by means of the rents previously referred to. The entire covering thus composed of perforated cells may be compared to an ordinary sponge, and, indeed, acts after the manner of a sponge. When it comes into contact with water in the liquid state, or more especially when it is moistened by atmospheric deposits, it imbibes instantaneously its fill of water. The deeper-lying living green cells of the root are then surrounded by a fluid envelope and are able to obtain from it as much water as they require.

But these roots also possess the power of condensing the aqueous vapour contained in the air. They act upon the moist air in which they are immersed in exactly the same way as spongy platinum or any other porous body. If the aërial roots of *Oncidium sphacelatum* are transferred from a chamber full of dry air to one full of moist air, they take up in 24 hours somewhat more than 8 per cent of their weight of water, those of *Epidendron elongatum* absorb 11 per cent, whilst in the case of many other tropical orchids the amount thus imbibed is doubtless much more considerable still.

The power of condensing aqueous vapour, and other gases as well, is of the greatest importance to these plants. The tree-bark serving as their substratum, to which they are fastened merely by a few fibres, is anything but a permanent source of water. Such water as the bark does contain reaches it, not from the interior of the trunk and indirectly from the soil in which the trunk has its roots, but from the atmosphere; that is to say, from the very source whence the epiphytes upon the bark must also derive their supply. Now, when on the occasion of a long-enduring uniform aërial temperature, there is a failure of atmospheric deposits, which is a regularly recurring circumstance in the habitat of the orchids in question, the sole source of water left is the vapour in the air, and the

PLATE III.



1. *Saccolobium guttatum*.

2. *Dendrobium nobile*.

3. *Phaius Wallichii*.



PLATE III.



TROPICAL EPIPHYTES IN CEYLON.



PLATE III.



TROPICAL EPIPHYTES IN CEYLON.



only possible method of acquiring that vapour is the condensation of it by the porous tissue investing the roots. In the event of the air around the orchid-plant containing temporarily but very little moisture, the porous tissue dries up, it is true, very quickly; its cells fill with air and their function as condensers is interrupted. But these air-filled cellular layers then form a medium of protection against excessive evaporation from the deeper strata of the root's tissues, which might be very dangerous in the case of this kind of epiphyte. There is a wide-spread impression that the tropical orchids grow in a perpetually moist atmosphere in the dark shade of primeval forests, and this preconception is fostered by pictures of tropical orchids representing these plants as living in the most obscure depths of woods. In reality, however, the orchids of the tropics are children of light. They thrive best in sunny spots in open country. Those species in particular which have their aerial roots invested each by a thick, white, papery, porous covering belong to regions where a long period of drought occurs regularly every year, and where, in consequence, vegetative activity is subject to periodical interruption, as it is in the cold winter season of the more inclement zones.

For epiphytes inhabiting these regions of the tropics a more expedient structure of root cannot easily be imagined. In the dry season the papery covering reinforces the safeguards against too profuse transpiration on the part of the living cells in the interior of the root, and in the wet season it provides for the continuous supply of the requisite quantity of water. In this sense the porous layer is to a certain extent a substitute for wet soil, or, in other words, the concealment of the living part of an aerial root in the saturated envelope is analogous to that of the root-fibres of land-plants in the damp earth. The manner in which the water reaches the inner cells of an aerial root from the saturated envelope is also quite characteristic. Under the porous tissue lies a layer composed of two kinds of cells of different sizes. The larger cells are elongated and have their external walls, which are adjacent to the porous tissue, thickened and hardly permeable by water. Between these lie smaller, thin-walled, succulent cells, which admit the water from the porous envelope, and should therefore be regarded as absorption-cells. It is also noteworthy that the porous, paper-like covering is discarded as soon as an aerial root is placed in earth. Most orchids with aerial roots perish, it is true, when they are treated like land-plants and planted in soil; but a few species, on occasion, bury their aerial roots spontaneously in the earth and push off their envelopes, and then the imbedded parts exercise the same functions as in the case of land-plants.

We have already mentioned that, in addition to thousands of orchids, several Aroideæ exhibit the porous, papery covering on their aerial roots. But still more frequently the air-roots of Aroids, which live as epiphytes upon trees, are furnished with a dense fringe of so-called root-hairs in a broad zone behind the growing-point. The hairs project on all sides from the roots, which are surrounded by air; they are crowded very closely together and give the parts affected a velvety appearance. Besides several Aroideæ, one of which (*Philodendron Lindenii*) is drawn on the left side of fig. 51, many other epiphytes, such as the South

American *Campelia Zanonia*, belonging to the Commelynaceæ, represented on the right side of the same figure, and also several tree-ferns, display this velvety



Fig. 51.—Aërial Roots with root-hairs; on the left *Philodendron Lindeni*, on the right *Campelia Zanonia*.

coating on their aerial roots. The roots of the tree-ferns are short, but spring in thousands from the thick stem, and are so closely packed that the whole surface is clothed as it were by a woven mantle of rootlets. After some time these aërial roots turn deep brown, whilst the hairs collapse and die, and both are converted

into a mouldering mass. But as soon as they perish other new air-roots, covered with golden-brown velvet, make their appearance and take their place. These aerial roots never reach the ground or adhere to any substratum, so that their hairs cannot contract an organic connection with a solid body. It is consequently also impossible in this case for the root-hairs to draw moisture from the soil in the capacity of absorption-cells.

These root-hairs, however, are scarcely ever in a position to take up even the atmospheric deposits. The various species of *Philodendron* and the other epiphytes referred to, have large leaves which cover the air-roots hanging from the stem like umbrellas, and every tree-fern also bears at the top of its stem a tuft of great fronds, which prevents falling rain from wetting the aerial roots. Moreover, the very plants whose air-roots exhibit a velvety coating occur in woods where the tops of the trees arch over the ground in lofty domes, and form a sheltering roof against deposits from the atmosphere. On the other hand, the air within these forests is saturated with aqueous vapour, and it is certain that the velvety roots have the power of condensing vapour, and that the root-hairs instantly suck up the condensed water and convey it to the deeper-lying layers of cells. The truth of this has been established by the results of repeated experiments. Thus, air-roots of the tree-fern *Todea barbata*, after being transferred from moderately damp air into a chamber full of vapour, condensed and absorbed in the space of twenty-four hours water amounting to 6·4 per cent of their weight. There is, therefore, no doubt that water may be acquired in this way also by plants, even though the instances may not be very numerous. All plants in which this kind of water-absorption has been hitherto observed grow in places where the air is very moist the whole year round, and where there is also no risk of the temperature falling below freezing-point. Under other conditions, especially in places where the air is periodically very dry, these plants would not be able to survive; for, although they possess organs for the condensation and absorption of water, they have no means of protection against the desiccation of these organs.

#### ABSORPTION OF RAIN AND DEW BY THE FOLIAGE-LEAVES.

The idea that plants absorb with their roots such water as they require is so intimately associated with our whole conception of plant-life, that this process is commonly adduced for the purpose of analogies of the most various kinds, and one looks upon the water-absorption effected by aerial roots in the manner just described really as a thing to be expected, notwithstanding the fact that in this case, as the above account shows, the phenomenon is not so simple as is usually supposed. We now turn to the consideration of land-plants. If the leaves of plants cultivated in pots become flaccid, water is poured as quickly as possible upon the dry soil with a view of supplying the roots which ramify in it with moisture. Nor does the result fail to be produced. In a short time the foliage becomes fresh and elastic again, the roots having discharged their function. Even in the open air, it is especially

the soil in which the roots are imbedded that a gardener waters on dry days, although incidentally he may pour the water over the aërial parts of the plants. He sees, however, that the water which falls in the form of rain or dew upon the foliage and stems normally runs off them at once, or else collects in drops, which trickle down whenever the plant is shaken by the wind, and are sucked up by the thirsty ground. This phenomenon must be due to the possession by the leaves of special contrivances to prevent their being wetted. It does not in any case support the idea that foliage is as well adapted for the absorption of water as experience has proved subterranean roots to be. This train of thought, which forces itself upon every unbiassed observer of the processes as they take place in nature, is certainly warranted in the majority of cases. Each absorption-cell on the roots buried in the earth has an easily permeable membrane, and, as is well known, water passes from damp earth through the cell-membranes into the interior of a plant with great rapidity. The water in the interior of the plant would be equally easily withdrawn through these cell-membranes by dry surroundings, but, as it is, this scarcely ever happens, in consequence of the roots being situated underground. In the case of aërial parts, especially the foliage-leaves, the circumstances are quite different. The leaves have to yield up to the air a portion at least of the water conducted from the roots, because, as will be more thoroughly explained later on, it is only by means of this evaporation that the entire machinery in the interior of the plant can be kept in motion. But this evaporation must not go too far; it must be in proper relation to the absorption of water by the subterranean roots, and be regulated to that end if the plant is not to run the risk of drying up altogether at times—an occurrence which flowering plants are unable to survive, although the mosses described in former pages have that power. Accordingly, in the case of the foliage-leaves of flowering plants, evaporation is confined to certain cells and groups of cells, and these, in addition, have contrivances by means of which evaporation can be entirely stopped on occasion of great drought. It stands to reason that all contrivances which make it impossible for water to pass from the interior of the leaves through the walls of the superficial cells into the surrounding air also hinder the entrance of water into the leaves from the atmosphere.

It would be altogether inconsistent with the system of arrangement of the subject adopted in this book if we were to discuss here all the contrivances serving to regulate the exhalation of water by leaves, and we must, therefore, confine ourselves to referring, by way of introduction, quite briefly, to the following facts, namely, that those pores on the surface of leaves which are known by the name of stomata, and are used as doors of egress by the exhaled water, do not admit rain or dew, or in general, any water in the liquid state; that the so-called cuticle covering the external walls of the epidermal cells in leaves is an additional barrier to both egress and ingress of water; that when, in particular, this cuticle is furnished with a wax-like coating, water does not adhere to the surface of cells so protected; and, lastly, that atmospheric moisture can only penetrate into the interior of the plant at parts of the leaves where the waxen incrustations are absent, where water remains adherent

to the leaf-surfaces, and they are distinctly wetted. But even cells and groups of cells of this kind usually act but for a short time as absorption-cells, and only when the necessity and craving for water is very great, or when there is an opportunity of acquiring nitrogenous compounds at the same time as the water; and here, again, special contrivances are always present which regulate this kind of water-absorption, and render it impossible whenever it is not truly advantageous.

At first one would suppose that amongst the cells composing the epidermis of foliage-leaves, those are best adapted to the absorption of water from the atmosphere which take the form of hairs. The superficial area being as great as possible, and the contained matter relatively little, one can scarcely in fact conceive a conformation better suited to the purpose of water-absorption. As, moreover, the area of contact between the cells of the leaf and of a hair is small, there would afterwards be but very little evaporation through the surface of the hair, of the water once sucked up by it and conducted into the interior of the leaf. In a word, these hairs on the surface of a leaf appear to be peculiarly adapted to the taking up of water, and not at all favourable to its exhalation. The hypothesis based on these observations is indeed entirely applicable to the case of hairs occurring on the leaflets of mosses, as has been already stated. But it does not hold in the case of the hair-like structures which spring from the leaf-surfaces of flowering plants. These are frequently not wetted at all by water; rain and dew roll off them in drops, and cannot, therefore, be absorbed by them. This is true even of many soft trichomes (hair-structures) which form investments upon leaves, and which seem to be more than any fitted for the absorption of water. For instance, experiments upon the woolly leaves of the Great Mullein (*Verbascum Thapseus*) have shown that they neither condense aqueous vapour nor take up water in liquid drops. Small importance must be attributed to the thickness of the cuticle, for sometimes it is the very cells which are equipped with a cuticle of considerable stoutness that are adapted to admit water, under certain circumstances, through their walls. On the other hand, much depends upon the presence of wax in the cuticle and upon the contents of the cells; that is to say, upon whether those contents in particular have a strong or weak affinity for water. If the cells of the hairs are full of air they are not adapted to the absorption of water.

If a hair is septate, i.e. consists of a simple series of cells, only the undermost or else only the uppermost cells of the series absorb water. Instances wherein it has been observed that the lowest cells alone in hairs of the kind become absorption-cells are afforded by the *Alfredia*, represented in fig. 14, by *Salvia argentea*, and several other steppe-plants. The same statement is made concerning the widely-distributed *Stellaria media*, the common Chickweed. This last has hairs on the internodes of the stem, running down in ridges from node to node. Usually only one side of the stem exhibits a ridge of hairs of the kind, and the ridge always terminates at the thickened node, whence springs a pair of opposite leaves. The stalks of these leaves are somewhat hollowed out and have their edges beset with hairs like lashes. The hairy ridges on the segments of the stem are readily wetted

by rain and retain a considerable quantity of water. The water that they cannot hold they conduct downwards to the ciliate axils of the next lower pair of leaves, where it is drawn through the lash-like hairs in due course and collected into a ring of water surrounding the node (see fig. 52<sup>3</sup>). If this accumulation of water becomes so voluminous and heavy that it cannot any longer be retained by the fringe of lashes, the surplus glides on to the unilateral ridge of hairs on the adjacent internode down to the pair of leaves below. Accordingly, after a shower every node from which leaves arise is seen to be inclosed in a water-bath, and the hairy



Fig. 52.—Hairs and Leaves which retain Dew and Rain.

<sup>1</sup> Dwarf Gentian (*Gentiana acaulis*).    <sup>2</sup> Lady's Mantle (*Alchemilla vulgaris*).    <sup>3</sup> Chickweed (*Stellaria media*).

ridges also are so soaked with water that they look like edgings of glass. All the individual cells in each of the hairs are full of protoplasm and cell-sap, but only the lowest, which are very short, really act as absorption-cells. When these cells become at all relaxed in dry air, the fact is indicated by the appearance on the external cell-wall of fine striæ (see fig. 53<sup>1</sup> and 53<sup>2</sup>). The protoplasts inhabiting them attract water, and after being relaxed in the manner referred to the cells regain their turgidity on being wetted, whilst the fine wrinkles on the outer membrane are in consequence immediately smoothed out. Although the upper cells of the hair possess a less thick cuticle, they, on the other hand, seem not to absorb any water, but to serve rather to conduct it by their surfaces.

This case is, as we have said, comparatively rare, and the corresponding absorp-

tion of water is not very considerable. But it often happens that the uppermost cells of a septate hair are developed into absorption-cells. The terminal cell is then usually spherical or ellipsoidal and larger than the rest, or else this cell is divided into two, four, or a greater number of cells, which together form a little head, whilst the lower cells constitute a stalk supporting it (see fig. 53<sup>3</sup> and 53<sup>4</sup>). In botanical terminology structures of this kind are named capitate or glandular hairs. The protoplasm in the cells of the head is, for the most part, of a dark colour, and the

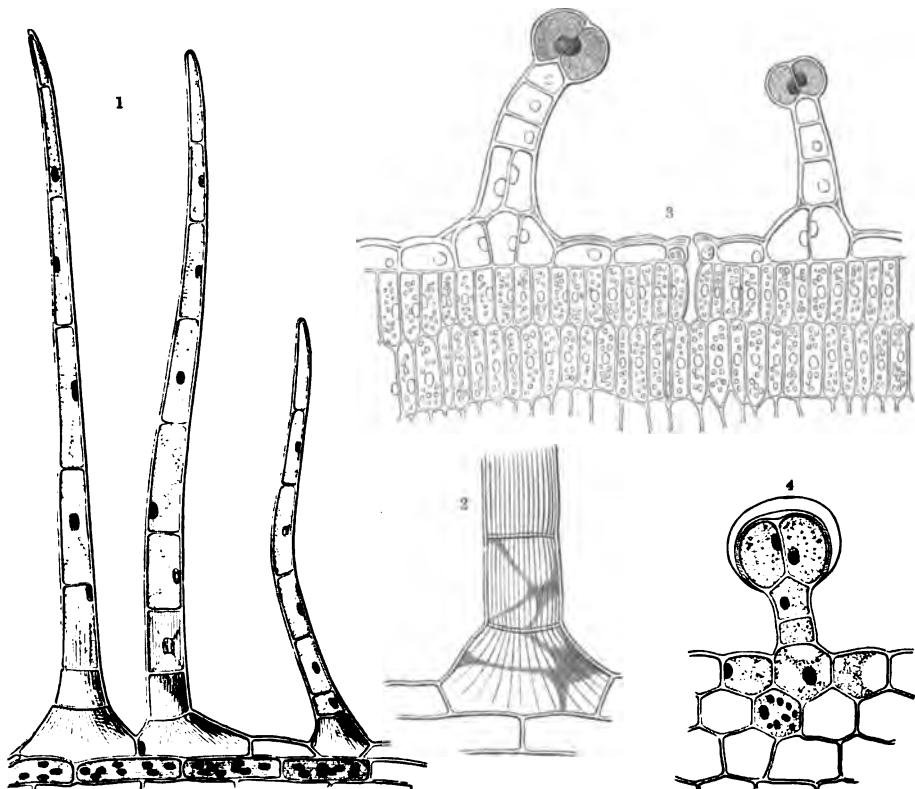


Fig. 53.—<sup>1</sup> Cauline hairs of *Stellaria media*;  $\times 110$ . <sup>2</sup> Lowest cells of the same hairs;  $\times 200$ . <sup>3</sup> Capitate hairs of *Centaurea Balsamita*;  $\times 150$ . <sup>4</sup> Capitate hairs of *Pelargonium lividum*;  $\times 150$ .

cell-membranes are readily permeable by water, which is attracted with great energy by the cell-contents. The cell-membrane is often very thick, it is true, but as soon as water comes into contact with it the outer layer is discarded, the inner layers swell up and the water passes through these swollen layers into the interior of the cell. This happens, for instance, in many pelargoniums and geraniums, wherein the capitate cells go through a process of excoriation on every occasion of the imbibition of water (see fig. 53<sup>4</sup>). In other plants the walls of the capitate cells are everywhere thin, and not only do the cell-contents consist of a viscid gum-like mass, but the external surface of the wall is also covered by a layer of viscid excretion. In many cases the viscid matter excreted by the glands spreads over the entire surface of the leaf, so that the latter feels sticky and looks as if it were

coated with varnish. Many plants which have their roots buried in crevices of rock and no small number of herbaceous steppe-plants are quite thickly covered with glandular hairs of the kind. *Centaurea Balsamita* (see fig. 53<sup>3</sup>), a plant occurring on the elevated steppes of Persia, may be selected as an example of the latter group. The advantage of the structure of capitate hairs is not far to seek. In dry weather the thick cuticle (*Pelargonium*) or the varnish coating (*Centaurea Balsamita*), as the case may be, prevents desiccation of the cells and groups of cells in question. But as soon as rain or dew falls, the cuticle and the coat of varnish take up water, and it is by their instrumentality that water reaches the interior of the cells. Thus, whilst the exhalation of water is hindered, its absorption is not.

Other epidermal cells of foliage-leaves besides trichomes are capable of acting as absorption-cells, although this action, for reasons already given, is very restricted, and is only had recourse to when the turgidity of the cells of the foliage-leaves has diminished, and the water exhaled by those cells is not being restored by the ordinary apparatus of conduction from the roots. If branches are cut from plants which bear no glandular or other form of hair on their leaves or stems—as, for instance, the leafy stem of *Thesium alpinum*—and the cut ends are closed with sealing-wax, and the branches left to wither, and, when quite withered, are immersed in water, they freshen up speedily and the leaves become tense again, the cells having recovered their turgidity. Here, then, decidedly absorption has taken place through the ordinary cuticularized epidermal cells. Certainly these epidermal cells in *Thesium* are not protected against wetting. Wherever the epidermal cells are not susceptible of being wetted owing to a coating of wax or any other contrivance there could naturally be no question of water being absorbed. This very circumstance, however, leads to the supposition that an important part in water absorption is to be attributed to the alternation of wettable and non-wettable parts on one and the same leaf. In the case of many foliage-leaves one can see that only those cells of the epidermis which lie above the veins of the leaf retain the water which comes upon them, that is to say, are wetted by it, whilst the water rolls off the intervening areas of the lamina. Indeed, there are in many instances contrivances obviously designed for the purpose of conducting water from parts of the epidermis not liable to be wetted to parts that can be moistened.

#### DEVELOPMENT OF ABSORPTION-CELLS IN SPECIAL CAVITIES AND GROOVES IN THE LEAVES.

The contrivances last described are all only adapted to rather a casual appropriation of water from the atmosphere. But besides these we find a number of other contrivances, which render it possible for every rolling dewdrop and every passing shower to be made of use to the utmost extent. These contrivances consist of a variety of depressions and excavations, in which rain and dew are collected and protected against rapid evaporation. Some species have deep hollows or channels, others little pits, whilst others again have basins, vesicular or bowl-

shaped structures, to collect and absorb the water; and the construction of the protective apparatus, which prevents too rapid evaporation into the air of water that has once flowed into the depressions, is as various as the form of the depressions themselves. A short account of the most striking of these structures will now be given.

Such water-collecting grooves as are closed, so as to form ducts, occur principally in petioles and in the rachises of compound leaves. For instance, in the Ash the leaf rachis, from which the leaflets arise, is furnished with a groove on its upper surface. Owing to the fact that the edges of this groove, which are strengthened by a so-called collenchymatous tissue, are bent up and curved over the groove, a duct or conduit pipe is produced, and this duct only gapes open at the places where the leaflets are inserted upon the rachis, and where, therefore, the drops of rain to which the leaflets are exposed flow off into the groove (see fig. 54<sup>1</sup>). The simple hairs and peltate groups of cells developed in the grooves and ducts (fig. 54<sup>2</sup> and 54<sup>3</sup>) are not merely transiently moistened, but inasmuch as the water is retained there for several days after a fall of rain, they are during that time immersed in a regular bath of water, and are able to absorb the moisture very gradually.

In many Gentianæ—most conspicuously in the large-flowered Dwarf Gentian (*Gentiana acaulis*)—the decussate pairs of radical leaves form a loose rosette (see fig. 52<sup>1</sup>). The larger dark-green blade of each leaf is flat and even, and only the pale-coloured base is fashioned into a groove. This groove is made deeper by the tissue of the leaf being puffed up round it, and as all the leaves of the rosette arise close together, the groove of each leaf is covered by the lamina above it. The rain or dew accumulated from the blade remains standing in this concealed nook for some time without evaporating, so that absorptive apparatus with the power of taking up water has plenty of time for the purpose. In this case the absorptive apparatus is in the hindmost extremity of the groove, and consists of long, club-shaped structures composed of extremely thin-walled cells (see fig. 54<sup>4</sup>), and these act so energetically that if leaves are cut off and left to fade, and if the cut surfaces are stopped with sealing-wax, and the whole then bathed with rain-water, they take up in twenty-four hours about 40 per cent of their weight of water. A similar phenomenon occurs in the case of a number of Bromeliaceæ which adhere by a few roots to the bark of trees in the tropics, and have grooved rosetted leaves, the latter covering one another, and being arranged in such a manner as to form a regular system of cisterns. At the bottom of each cistern there are special groups of thin-walled cells which suck up any water that flows in when rain falls.

On the under surface of the leaves of the Cow-berry (*Vaccinium Vitis-Idaea*) little depressions are formed, and in the middle of each depression there is a club-shaped structure composed of small thin-walled cells, which contain slimy, viscid substances and act as absorbent organs. The rain which falls upon the upper surface of the leaf gets drawn over the edges on to the under surface, fills the small depressions occurring there, and is taken up by the absorptive apparatus. A

similar contrivance is also exhibited by the leaves of alpine roses and those of the American *Bacharis*. For instance, on the under surface of the leaves of the Alpine Rose (*Rhododendron hirsutum*) there is a large number of discoid glands (fig. 54<sup>5</sup>), each of which is supported on a short stalk and sunk in a little hollow (fig. 54<sup>6</sup>). The cells composing the gland are arranged radially, and contain slimy, resinous matters capable of swelling up. These contents are also excreted, and then cover the entire glandular disc, and often even the whole surface of the leaf in the form

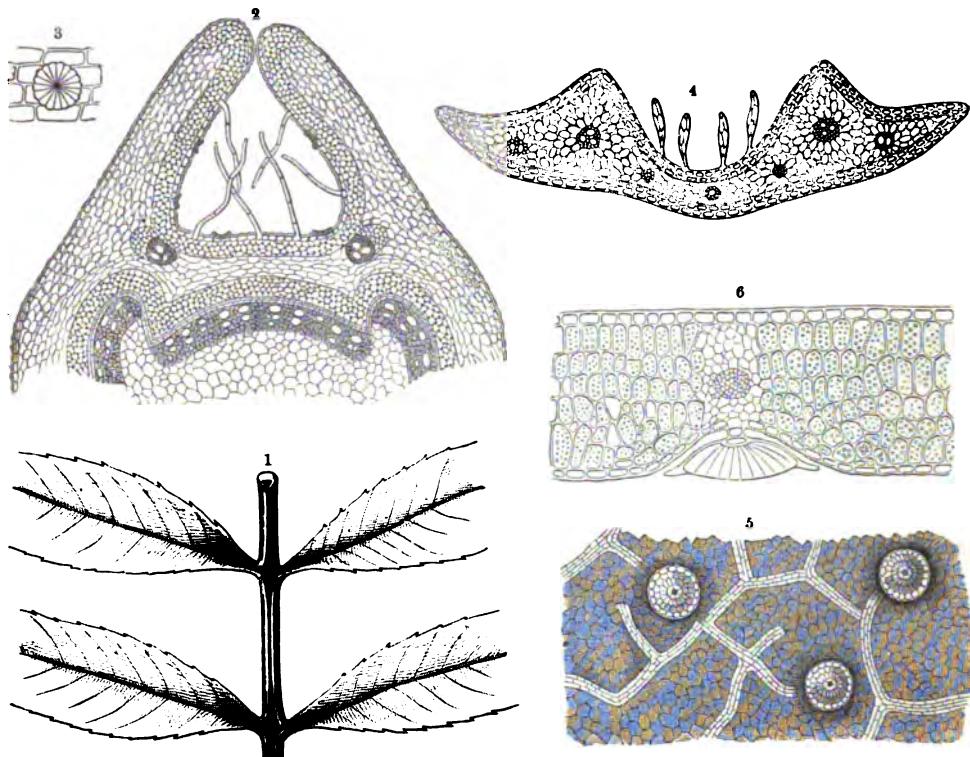


Fig. 54.—Absorption of Water by Foliage-leaves.

<sup>1</sup> Grooved rachis of the ash-leaf. <sup>2</sup> Section through the same;  $\times 30$ . <sup>3</sup> Peltate group of cells from the groove. <sup>4</sup> Section through the base of a leaf of the Dwarf Gentian;  $\times 20$ . <sup>5</sup> Under side of a leaf of *Rhododendron hirsutum*;  $\times 30$ . <sup>6</sup> Section through a leaf of *Rhododendron hirsutum*.

of a light-brown crumbly crust. When drops of rain fall upon Alpine Rose leaves, the whole of the upper surfaces, in each case, is in the first place moistened; but without delay, and partly through the action of the hairs fringing the margin, the water soaks on to the under side of the leaf. As soon as it reaches the glands it is taken up by the crumbly incrustation mentioned above, which swells up in consequence. The little cavities in which the glands are situated also fill with water, and each gland is then immersed, as it were, in a bath, and able to absorb as much moisture as is required. Owing to the glands being invariably developed above the vascular bundles of the leaf (see fig. 54<sup>6</sup>), the water that is absorbed can be conducted without delay by them to the places where it is required. As soon as the leaves of alpine roses become dry again, the mass of resinous mucilage again

forms a dry crust over the glands and protects their tender-walled cells from too great evaporation.

Very remarkable also are the structures adapted to absorption on the leaves of saxifrages belonging to the group *Aizoon*, and on those of a large proportion of the Plumbagineæ. The saxifrages in question have little depressions visible to the naked eye upon the upper surface of the leaves behind the apex, and along the margins. When the margin is dentate or crenate, as, for instance, in *Saxifraga*

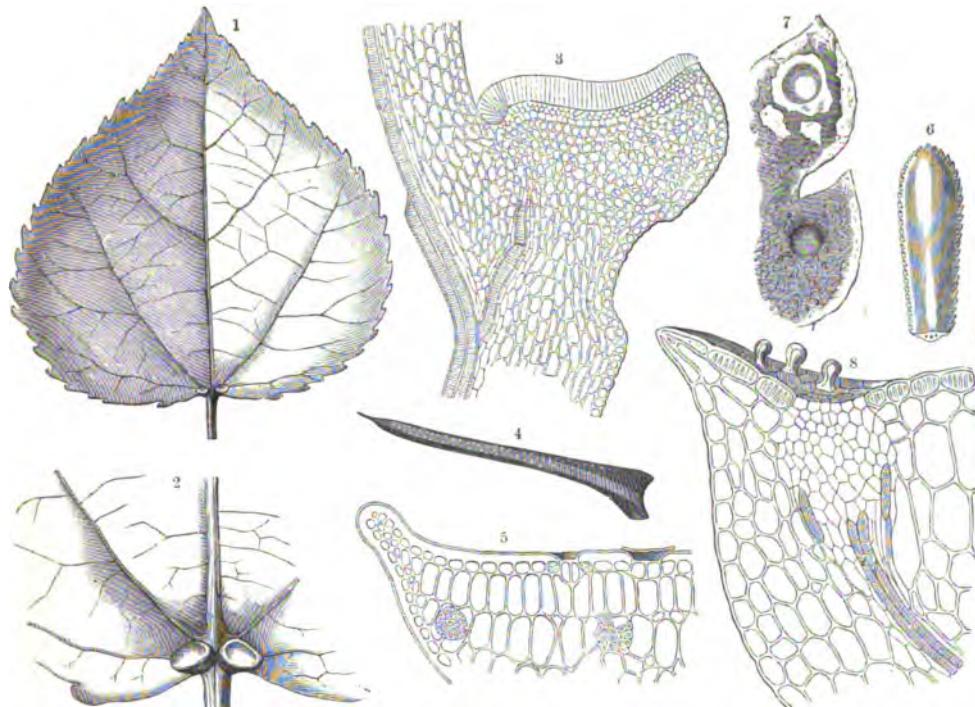


Fig. 55.—Absorptive Cavities and Cups on Foliage-leaves.

<sup>1</sup> Leaf from a shoot of the Aspen. <sup>2</sup> The base of this leaf;  $\times 8$ . <sup>3</sup> Section through an absorption-cup;  $\times 25$ . <sup>4</sup> Leaf of *Acantholimon Senganaense*. <sup>5</sup> Section through part of this leaf;  $\times 110$ . <sup>6</sup> Leaf of the Evergreen Saxifrage (*Saxifraga Aizoon*). <sup>7</sup> Two teeth from the margin of this leaf. The absorptive cavity in the upper tooth incrusted with lime; the lower one with the incrustation removed. <sup>8</sup> Section through a tooth and its absorptive cavity;  $\times 110$ .

*Aizoon* (see fig. 55<sup>6</sup>), one of these cavities occurs in the middle of each tooth. The cells forming the outer edge of the tooth or scallop are always much thickened, firm, and rigid; but the median portion of the leaf as a whole is fleshy, and composed of a bulky large-celled parenchyma. The vascular bundle, after entering the leaf at its base, divides into a number of lateral bundles which either run towards the margin without further ramification (as in *Saxicæsia*), or else form a net-work by uniting one with another in their course (as in *Saxifraga Aizoon*). These lateral bundles terminate in the marginal teeth of the leaf and immediately beneath the little cavities which occur there, whilst the extremity of each bundle swells into a knob or pear-shaped enlargement strongly resembling the roundish groups of spirally-thickened cells in the tentacles of the Sun-dew

(cf. fig. 26<sup>1</sup>). The bottom of each depression is made up of cells with very thin external walls, and the function of these cells is to suck up the water that flows into the cavity. It is obvious that the absorbed water passes thence into the enlarged extremities of the branches of the vascular bundles, and may then be conducted to other parts of the leaf. Seeing that all these saxifrages have their habitat in crevices of rocks on sunny declivities, they are much exposed to desiccation in times of drought. The epidermal cells of the medial area and those of the extreme edge are no doubt protected by a very thick cuticle (see fig. 55<sup>8</sup>); but in the case of the thin-walled cells at the bottom of the depression there is the danger of as much or even more water escaping through them, in the form of vapour, than has been previously taken in during the prevalence of rain.

In order to prevent this loss of moisture recourse is had to a very remarkable contrivance for closing the cavity, viz., an incrustation of carbonate of lime. In many saxifrages this crust covers the whole face of the leaf, in others only the margin, or the spot where the depression occurs. In the latter case it looks like a lid over the cavity. At that spot the crust is always thickened, and sometimes it forms a regular stopper which fills up the entire cavity. It rests upon the epidermis of the leaf, but is not adnate thereto, and may be removed with a needle. When a leaf is bent the crust is ruptured and breaks up into irregular plates and scales, and a strong gust of wind would then easily strip off the fragments and blow them away. In species subject to this danger, as, for instance, *Saxifraga Aizoon*, in which the rosetted leaves curl strongly upwards and inwards in dry weather, the crust of lime is held fast by peculiar plugs which arise from individual epidermal cells projecting above the rest in the form of papillæ (see fig. 55<sup>8</sup>). These plugs are found principally on the side walls of the cavities, but are also scattered everywhere on the epidermis of the margin of the leaf. They are so incrusted with the lime that the latter cannot easily fall off, and a comparatively strong pressure must be applied with the needle to detach it from the substratum. The calcium carbonate of which these crusts consist is excreted in solution by the plant from pores occurring at the bottom of the depressions. The pores are constructed like ordinary stomata, but are, as a rule, somewhat bigger, and it is not improbable that, when once the lime crust has formed from the excreted solution, they take part in the function of transpiration.

There is scarcely any need for further explanation of the manner in which the apparatus here described acts. When rain or dew falls on a saxifrage leaf the whole upper surface is moistened directly, whilst the water soaks under the crust of lime, and, diffusing itself there, fills in a moment the depressions, and is taken up by the absorption-cells situated at the bottom of the latter. The calcareous stopper imbedded in each cavity is only upheaved by this process to a trifling extent. In dry weather the crust is appressed closely to the epidermal cells, and the stopper descends again and impedes the evaporation of water from the thin-walled cells within the cavities.

The absorptive organs on the leaves of *Acantholimon*, *Goniolimon*, and a few

other Plumbagineæ, resemble in an extraordinary degree those pertaining to saxifrages. The depressions are here found uniformly distributed over the entire surface of a leaf, and when they are closed by a crust or scale composed of calcium carbonate, the leaves are dotted with white spots, as may be seen in the drawing of a leaf of *Acantholimon Senganaense* given in fig. 55<sup>4</sup>. Upon the calcareous scale being removed, a little cavity is revealed beneath, and one observes that the floor of this cavity is composed of from four to eight cells, separated by radial partition-walls, and with exceedingly thin and delicate outer walls. The other epidermal cells adjoining the cavity are, on the contrary, always furnished with a thick cuticle (see fig. 55<sup>5</sup>). Whenever water is being copiously supplied to the roots, and the turgidity of the cells in the leaves is great, the cells forming the floor of the cavity excrete bicarbonate of lime in solution. Part of the carbonic acid escapes into the air, and the insoluble mono-carbonate of lime in the water then forms a crust, which fills and covers the cavity, and often even spreads over the whole leaf, constituting a coherent calcareous coat.

All Plumbagineæ which exhibit this contrivance—that is to say, the various species of *Acantholimon*, *Goniolimon*, and *Statice*—inhabit steppes and deserts, where in summer no rain falls for months together, and the soil becomes dry to a considerable depth, so that extremely little water is available for the roots. Although the rigid leaves are protected by a thick cuticle, and by crusts and scales of lime against excessive evaporation of their aqueous contents, still it is difficult to avoid some slight loss of water, especially when the noon-day sun beats down upon the steppe, and, owing to the extremely arid nature of the soil, it is scarcely possible to replace this loss, however small it may be, by absorption from the earth on the part of the suction-cells on the roots. All the more welcome to plants of the kind is the dew which sometimes falls copiously on steppes and in deserts in the course of the night; it wets the rigid leaves, and, soaking immediately underneath the crusts and scales of lime to the thin-walled cells at the bottom of the cavities, is absorbed with avidity by them. When drought returns with the day, the scales of lime close tightly down like lids on the epidermis beneath, and, so far as possible, prevent evaporation. In particular, they impede the exhalation of water from the thin-walled cells at the bottom of the cavities—a loss which would otherwise be quite inevitable, and would be followed by a rapid desiccation of the entire plant. To prevent the calcareous lids from dropping off, there are either, as in *Saxifraga Aizoon*, papilliform or conical projections from cells in the immediate vicinity of the cavities, which projections often have hooked ends and confine the crust of lime, or else each cavity is somewhat contracted at the top and enlarged below, so that the lime stopper, being shaped according to the contour of the cavity, cannot fall out.

A significance similar to that attributed to calcium carbonate excretions belongs also to the saline crusts which are found covering the leaves of a few plants growing on the arid ground of steppes and deserts in the neighbourhood of salt lakes and on the dry tracts of land near the seashore. Owing to the fact that in these

situations crystals of salt are sometimes to be seen separated out from the soil, and lying as a white efflorescence upon the ground, it used formerly to be believed that the salt incrusting leaves and stems was derived, not from the plants in question, but from the soil around, and had only spread from there over the various plant-members. But this is not the case. As a matter of fact, the salt observed on the leaves and stems of *Frankenia*, *Reaumuria*, *Hypericopsis persica*, and a few species of *Tamarix* and *Statice*, is produced from the substance of the leaves. It is excreted in just the same way as the crust of lime, above described, is from the leaves of saxifrages. To the naked eye the surfaces of the leaves in all the plants enumerated have a punctate appearance. On closer inspection, it is evident that, corresponding to each dot, there is a little cavity, the deepest part of which is constructed of cells with extremely delicate external walls. In quite young leaves only a single thin-walled cell of the kind is to be seen at the bottom of each shallow depression. But this divides, and, by the time the leaf is full-grown, from two to four cells are seen to have arisen by division of the one cell. Stomata are, in addition, intercalated in the membrane in the neighbourhood of these thin-walled cells, and, in the rainy season, when there is no lack of water in the habitats of the plants in question, a watery juice, containing a large amount of salts in solution, exudes from these stomata. The saline solution soaks over the whole surface of the leaf, and in a dry atmosphere crystals form from it and adhere to the leaf in the form of little gland-like patches or continuous crusts.

If these tamarisks, frankenias, and reaumurias are observed during a rainless season, the crystals of salt are seen under the noon-day sun glittering on the leaves and stems, and may be detached in the form of a fine crystalline powder. But if the same place is visited after a clear night, no trace of crystals is to be seen; the little leaflets have a green appearance, but they are covered with a liquid with a bitter salt taste,<sup>1</sup> and are damp and greasy to the touch. The crystals have attracted moisture from the air during the night, and have deliquesced, and the saline solution not only covers the whole of the leaf, but also fills the little cavities visible as dots to the naked eye. The thin-walled cells at the bottom of the cavities differ from the rest of the epidermal cells and the guard-cells of the stomata, in that they are susceptible of being wetted, and they may act as absorption-cells, and allow the water, attracted by the salts from the air, to pass through their thin walls into the interior of the leaves.

When the air dries under the rising sun, crystals are again formed from the solution of salts, and, covering the leaves once more in the form of crusts, fill up the depressions and protect the plants during the hot hours of the day from excessive evaporation. Whilst, therefore, in the dewy night these plants are indebted to their salt crusts for water, they are in the day-time preserved from desiccation by the action of the same contrivance.

<sup>1</sup>The salt inocrustations which were removed from plants of *Frankenia hispida*, collected on a Persian salt-steppe, consisted principally of common salt (chloride of sodium). They contained in smaller quantities, gypsum, magnesium sulphate, calcium chloride, and magnesium chloride.

It is also worthy of mention that papillæ are developed near the absorption-cells, with a view to the retention of the salt crystals, similar to those which hold the calcareous incrustations on the leaves of saxifrages and *Acantholimon*. The leaves of plants covered with crystals of salt are also for the most part furnished with little bristles, to which the salt adheres so firmly that it is not readily detached, even by violent shaking.

But however striking the analogy between the development and significance of lime crusts and salt crusts respectfully, there is the essential difference that the former have not, like the latter, the power of attracting moisture from the air. And on this particular stress must be laid. In the hilly and mountainous tracts on the shores of salt-lakes or of the sea, where tamarisks and frankenias are especially wont to live, the sandy ground dries up to such an extent in the height of summer that it is scarcely conceivable how plants growing in it are able to preserve their vitality. The proximity of the sea has no immediate effect on the moisture of the ground in such situations. The sea-water does not penetrate into the ground far beyond the high-water line, and it is out of the question that the layers of soil serving as substratum to the frankenias and tamarisks should be irrigated by subterranean water. When in summer there is an absence of rain for months together, these plants—even though in close proximity to the sea—would necessarily perish of drought. Only the circumstance that they turn to account the moisture of the atmosphere by means of the excreted salts renders it possible for them to flourish in these most inhospitable of all inhospitable sites.

Many plants which are periodically exposed to great dryness have the tips of the teeth on the leaf-margins thickened into little cones or warts. They also glitter somewhat and at times are sticky. The glitter and viscosity are due to a resinous slimy substance, which often contains sugar and tastes sweet. This substance covers the teeth and sometimes spreads from the teeth inwards to a great distance over the face of the leaf in the form of a delicate film-like varnish. The greatest resemblance exists between this varnish (sometimes known as "balsam") and the secretions of the glands on the leaves of the Alpine Rose and of the glandular hairs on those of *Centaurea Balsamita*. It is excreted by special cells, which are intercalated in the epidermis of the foliar teeth, and are at once marked out from the other cells of the epidermis by the facts that their protoplasm is of a brownish colour and that their external walls are easily permeable by water. The excretion of the varnish-like layer takes place at a time when the entire plant is distended with sap, chiefly, therefore, in the spring. When summer is at its height the varnish dries and thenceforward affords an excellent preservative from the risk of too much evaporation from the cells it covers, and especially from those situated on the teeth of the leaves by which it was excreted. But if this dried film of varnish is wetted it saturates itself quickly with water and renders moisture accessible to the cells beneath it. Thus its value is similar to that of the crusts of lime and salt on the leaves of the plants above described. When moist it effects the absorption of water, when dry it guards against desiccation.

The reason for the contrivance just described being exhibited especially by the marginal teeth of the leaf, lies in the fact that dew is deposited particularly at those spots. If one looks at the leaves of the dwarf almond and plum trees in the steppe-districts, after clear summer nights, one finds a dewdrop suspended to every tooth on the margins; but by noon all the teeth are dry again and protected from loss of water by the coat of varnish. Moreover, not steppe-plants alone, but very many plants which grow in poor sandy soil on the banks of streams and rivers, exhibit this contrivance for the direct absorption of water from the atmosphere. Instances are afforded by the Sweet Willow, the Crack-willow, Poplars, the Guelder-rose, the Bird-cherry, and many others. It is at once evident that this contrivance is observed chiefly on the leaves of trees, shrubs, and tall herbs, whilst incrustations of lime occur only on shorter plants with rosulate leaves spread out on the ground, or with rigid acicular leaf-structures. The grounds of this distinction may well reside in the fact that the weight of a crust of lime is many times as great as that of the dry film of varnish. A load capable of being borne without hazard by the leaves of a *Statice* plant, they being spread out on the ground, or by the rosettes of *Saxifraga Aizoon*, would be unfit for the leaves of a Cherry or Apricot tree, or for those of the Sweet Willow, or the Crack-willow; indeed the branches of these trees would break down under the burden if their leaves were incrusted with lime.

In many cases only a few of the marginal teeth of the leaf are transformed into absorbent apparatus, and special contrivances then always exist to convey rain and dew to those teeth. The Aspen (*Populus tremula*) serves as a very good example of this. This tree has, as is generally known, two kinds of leaves. Those arising from the branches of the crown have long petioles and laminae of roundish outline and with somewhat sinuate margins; those which are borne by the radical shoots have shorter stalks and larger sub-triangular laminae sloping outwards; and the whole leaf is so placed and its margin so curved as to oblige the rain which strikes the upper surface in its descent to flow down towards the petiole (see fig. 55<sup>1</sup>). Now, situated exactly on the boundary of lamina and petiole are two cup-shaped structures (fig. 55<sup>2</sup>) originating from the lowest teeth of the leaf, and so arranged that every drop of rain descending from the lamina must encounter their shallow cavities and fill them with water. These cups are brown in colour and the size of a grain of millet; and the cells of their epidermis are furnished with a thick cuticle. Only the cells lining the shallow depression of each cup have thin walls, and they excrete a sweet-tasting, slimy, resinous substance which in dry weather films over the cavity like a varnish, and protects, at all events, the cells lying beneath it against an injurious desiccation. When, however, this coat is itself in contact with water it swells up, and the moisture is then absorbed by the cells in the pit-like depression and is transmitted to the vessels running underneath the cups (see fig. 55<sup>3</sup>).

A number of tall herbs, principally of the group of Compositæ, have, like the Aspen, leaf-teeth which are developed at the part where petiole and lamina join and act as organs of absorption. In some, besides, the margin of the green lamina extends in the form of a narrow ridge down the pale canaliculate petiole; and, when

this is the case, teeth of the kind are found on this narrow green ridge which runs along the groove. In *Telekia*, a handsome herbaceous plant of wide distribution in the south-east of Europe, these teeth—conical or club-shaped—springing from the margin of the petiole-groove are incurved, and are in general so placed that their blunt apices project into the groove. But precisely on these obtuse tips of the teeth are situated cells with very thin outer walls easily permeable to water, and having contents with a strong attraction for it. Thus, as soon as the groove of the



Fig. 50.—Water-receptacles.  
1 In a Teasel, *Dipsacus laciniatus*.      2 In the American *Silphium perfoliatum*.

petiole is filled with rain, collected from the surface of the leaf, the tips of the conical teeth are moistened, and they suck up the water.

Lastly, we have to mention the curious receptacles appertaining to foliage-leaves in which water from the atmosphere accumulates and continues to stand for weeks without being protected from evaporation by the excretion of special substances. Any region or portion of the leaf may participate in their construction. In *Saxifraga peltata* the lamina is shaped like a shield and forms a shallow plate with the concave surface turned to the sky. In the Cloud-berry (*Rubus Chamaemorus*) the formation of basins is brought about by the margins of the reniform lamina being superimposed over one another as if to make a spathe. In the various species of Winter-green, especially in *Pyrola uniflora*, the pale caudine leaves,

inserted above to the green leaves, are metamorphosed into little saucers. In one species of Teasel, *Dipsacus laciniatus* (see fig. 56<sup>1</sup>), and in the North American *Silphium perfoliatum* (fig. 56<sup>2</sup>) the two sheathing portions (vaginae) of every pair of opposite leaves are connate and form comparatively large and deep funnel-shaped basins, from the middle of which rises the next higher internode of the stem. In several Meadow-rues (*Thalictrum galiosides* and *T. simplex*) the secondary leaflets, which are opposite one another and shut close, almost like the valves of a mussel, are moulded so as to form cavities for the retention of water, and in many Umbelliferae, such as *Heracleum* and *Angelica*, the vagina of each individual leaf is ventricose or inflated, thus forming a sac enveloping the segment of the stem which stands above it.

These basins, saucers, and dishes are always so placed, relatively to their surroundings, that the water derived from rain and dew is directed into them from the surfaces of the leaves, or by the segment of the stem which rises from their centres, and thus it is that the depressions are filled. Whether in all cases much of the water accumulated is absorbed is certainly open to doubt. In the case of the leaves of the *Alchemilla* (fig. 52<sup>2</sup>), which exhibit the phenomenon so conspicuously that the plant has received the popular name of Dew-cup; the absorption of water is, at anyrate, very inconsiderable, and here the retention of the dew secures advantages of a different kind to which we shall presently have occasion to return. On the other hand, it is established that in the case of basins belonging to tall herbaceous plants, particularly such as grow on steppes and prairies where often no rain falls for a long interval, the water collected is absorbed by the glandular hairs and thin-walled epidermal cells developed within them. The fact of this absorption may be proved by a very simple experiment. Let a stem of the *Silphium*, represented in fig. 56<sup>2</sup>, be cut off beneath the pair of connate leaves, which form a basin by their union, and let the cut surface be closed with sealing-wax, so that no water can be taken up by the stem from below. If the water accumulated in the basin is now emptied out, the leaves shortly become flaccid and droop; but if the basin is left full of water, the leaves preserve their freshness a long while and do not begin to wither until all the water has evaporated and disappeared from the basin. If oil is poured upon the collection of water in the basin, so that evaporation from the latter is impeded, a constant diminution of the water in the basin is observed notwithstanding; this leads to the conclusion that the water in question is really taken up by the absorption-cells at the bottom of the basin and conveyed to the tissue of the leaf.

The first thing that strikes one on surveying once more all the plants possessing on their aerial organs special contrivances for water-absorption is that a large proportion of them have taken up their abode in swamps and on the banks of rivers and streams, or if not there, at all events in situations where no danger exists of the ground being thoroughly dried up. No doubt this appears to be inconsistent. How are we to explain the fact that Gentianæ, ashes, willows, alpine roses, bog-mosses, &c., are still in need of water from the atmosphere, when they all

grow either in damp meadows, peat-bogs, on the borders of never-failing springs, or in ever-moist ravines, where their requirements in respect of nutrient water and imbibitious water can be supplied all around by means of the roots? A glance at the company in which these plants occur may perhaps lead to a solution of the problem. In the damp meadows and along the margins of springs where gentians, the Sweet-willow, and plants of that kind are found, the Butterwort (*Pinguicula*), which has been described in earlier pages amongst carnivorous plants, is never absent; whilst wherever the pale cushions of the Bog-moss spring, there also the Sun-dew is certain to spread out its tentacles for the capture of prey.

With reference to community of site the assumption is warranted that all these plants which flourish under identical conditions of life endeavour to acquire the same material by means of their aerial parts. Now, this material cannot well be other than nitrogen, of which they do not find a sufficient store in the substratum. What then is more natural than that those plants, which are not adapted to the capture of animals, should use their aerial organs, when these are moistened with rain or dew, to take up direct nitric acid and ammonia, which are contained—though in small traces only—in the atmospheric deposits, instead of waiting till compounds of such great importance to them penetrate into the ground where they may chance to be detained at spots whence the roots could only obtain them after long delay and by a highly complicated process? When one considers that plants, growing amid the sand and detritus of steppes, on ledges, and in crevices of steep rocks, or epiphytic on the bark of trees, are also able to acquire little or no nitrogenous food from the substratum by means of their roots, their especial equipment with apparatus for the absorption of atmospheric water becomes explicable on the ground of the latter being the medium of solution and transport of nitrogenous compounds. In the case of epiphytes and of plants growing on steppes or rocks, there is the additional consideration that a supply of pure water, supplemental to that which can be withdrawn from the substratum, must be very welcome to them in dry weather, and that at such times it is a great advantage for the atmospheric water to be absorbed directly by the aerial organs instead of reaching them in a roundabout manner through the substratum.

If this idea is justified, the atmospheric moisture taken up by the aerial organs with the help of the above-described contrivances, would be of value to the plant chiefly in being a carrier of nitrogenous compounds, and in this acceptation would have to be looked upon as water of imbibition. Whether it is also used, at least in part, as food-material can neither be asserted nor controverted. A separate absorption of water which serves only for motive power, and of that which is in addition employed in the construction of organic compounds does not take place in a plant, it is not possible to make any *a priori* statement concerning the moisture taken up, as to which part it has to play in the plant. Most probably the allotment of functions is not at all uniform, but varies considerably according to conditions of time, place, and requirement.

On a former occasion it has been mentioned that small animals are not  
Vol. I. 16

infrequently killed accidentally in the water filling the larger kinds of basins formed as parts of foliage-leaves, that pollen, spores, and particles of earth also are blown by the wind into these basins, and that, after the ensuing solution and decomposition of the organic and mineral bodies in question, the water exhibits a brownish colour and contains organic compounds as well as food-salts in solution. It is not necessary to repeat that these compounds are able to pass into the interior of the plant with the water through the action of the absorption-cells which are never absent from the bottom of the basins; but it seems proper to consider specially in this connection the most conspicuous cases of the phenomenon which have been observed. The greatest quantity of matter, dissolved and undissolved, is found in the flat, saucer-shaped laminæ of *Saxifraga peltata*, which grows on the sites of springs in the Sierra Nevada of North America. The water in these saucers is sometimes coloured quite a dark brown by the presence of decayed beetles, wasps, centipedes, fallen leaves, and animal excreta; and when it evaporates a regular crust is left behind at the bottom of the reservoir. Three days after rain I still found in the inflated *vagina* of *Heracleum palmatum*, a species of cow-parsnip, a pool of brown water 2 cm. deep, and at the bottom a deposit of blackish, oily mud in which the remains of decayed earwigs, beetles, and spiders, were still recognizable. The same thing is observed in the cisterns of Bromeliaceæ and in the water-basins of *Dipsacus laciniatus* and *Silphium perfoliatum* (fig. 56), and it is interesting to find there are cells also at the bottom of the basins of the *Dipsacus* in question from which protoplasmic threads radiate forth, as in the case of the chambers of the Toothwort, and that numberless putrefactive bacteria always make their appearance in the water in these basins. The quantity of organic residue is less considerable in the saucer-shaped leaves of pelargoniums, but, on the other hand, earthy particles are frequently met with in them to such an extent that, when the water has evaporated, the concave surface of the leaf is covered with an ashen-gray layer of earth.

Observations of this nature establish the conviction that no sharp line of demarcation exists in respect of the absorption of water either between carnivorous plants and land plants, or between land plants and saprophytes, or between saprophytes and carnivorous plants; and they lead further to the conclusion that water, mineral food-salts, and organic compounds are susceptible of being taken up not only by subterranean but also by aërial absorptive apparatus.

---

## 6. SYMBIOSIS.

Lichens.—Cases of symbiosis of Flowering Plants having green leaves with the mycelia of Fungi destitute of chlorophyll.—Monotropa.—Plants and Animals considered as a vast symbiotic community.

### LICHENS.

In describing the vegetation of a limited area botanical writers are apt to designate the various species of plants as "denizens" of the country in question. The conditions under which the plants live are likened to political institutions, and the relations existing amongst the plants themselves are compared to the life and strife of human society. By no means the least important factor in the suggestion of these analogies is the circumstance that often as a matter of fact one has opportunities of seeing how the species of plants which live together in a locality are dependent in various ways upon one another; how they exist in continual conflict for the food, the ground, for light and air; how some are preyed upon and oppressed by others, whilst others are supported and protected by their neighbours; and how, not infrequently, quite different species join together in order to attain some mutual advantage.

As regards the preying of one upon another the subject has been treated in detail in a previous chapter, and it was also stated then that the term parasite can only be applied to those plants which withdraw materials from the living parts of other organisms without rendering a reciprocal service in return. The host attacked by a parasite supplies food and drink without being in any way compensated. One might suppose that nothing would be simpler and easier than to ascertain the existence of this relationship, and yet many difficulties are encountered in the determination of parasitism in individual cases. The main difficulty is due to the fact that one cannot always say with certainty whether the host does not perhaps get some advantage from the parasite which drains its juices. Should this be the case, however, the latter would be no longer a parasite, and the relationship between the two would rather be that of simple commerce and mutual assistance, an amicable association for the benefit of both.

Whilst discussing the second series of parasites, the fact was mentioned that the plants upon which the various species of Eyebright fasten their suckers suffer no apparent injury as a consequence of this connection. The rootlet organically united to the suckers does, it is true, die away in the autumn; but the Eyebright also withers at that season, and it is not inconceivable that the useful substances existing in the green leaves of the Eyebright may be transferred, shortly before the latter withers, to the host-plant and deposited there at a convenient time in the permanent part of the root as reserve-material, and that in this way the host-plant ultimately derives benefit from the so-called parasite. The idea here suggested as a possibility for the case of Eyebright and the grasses connected with it is an ascertained fact in the case of some other plants. For plants are known which unite to

form a single organism and thenceforward so co-operate in their functions that ultimately both derive advantage from the arrangement. The one takes food-stuffs from the substratum and from the air and transmits them to the other; whilst, in the green cells of the other, the raw material is worked up, under the influence of sunlight, into organic compounds. The organic compounds thus created are used by both for the further production of organs, and therefore a connection such as this must be looked upon as a true case of symbiosis, i.e. associated existence for purposes of nutrition.

The first place amongst social communities of the kind must be assigned to Lichens, a section of Cryptogams possessing an extraordinarily large number of species and differentiated into thousands of forms, representatives of which are

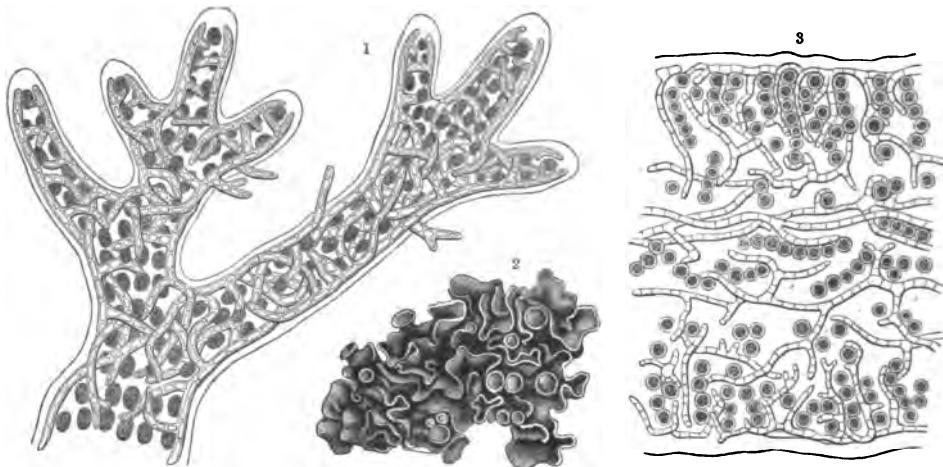


Fig. 57.—Gelatinous Lichens.

<sup>1</sup> *Ephelia Kernerii*;  $\times 450$ . <sup>2</sup> *Collema pulporum*; natural size. <sup>3</sup> Section through *Collema pulporum*;  $\times 450$ .

everywhere distributed, from the sea-shore to the highest mountain peaks yet scaled by man, and from the tropics to the arctic and antarctic zones.

The partners in the Lichen communities appear to be, on the one hand, groups and filaments of round, ellipsoidal, or discoid green cells belonging to plant species included under the general name of *Algæ*; and, on the other hand, pale, tubular cells or hyphae, which are destitute of chlorophyll, and pertain to species of plants comprised under the general name of *Fungi* (see fig. 58).

The form assumed by a large proportion of these lichens is that of incrustations on stones, earth, bark, or old wood-work; the entire structure of the lichen is either ensconced and imbedded in the depressions of weathered surfaces of stone, or else between the cell-walls of dead fragments of wood and bark, so that it often happens that attention is only drawn to its presence by the altered colour of the substratum, or by the fructifications which lift their heads above the substratum.

Lichens of the kind are termed Crustaceous Lichens, and the wide-spread Graphic Lichen (*Lecidea geographica*) may serve as an example. A second great group nearly allied to the first is that of Foliaceous Lichens. The form of the

vegetative body in these is best compared to the foliage-leaves of the Curled Mint, with their corrugated or sinuate margins, or to those of *Malva rotundifolia*. It may also be described as a number of lobes radiating irregularly and bifurcating repeatedly, and only lightly joined to the substratum by root-like fringes, and therefore capable of being readily loosened and detached. The light-grey *Parmelia saxatilis*, which bear brown saucer-shaped fructifications, may be taken as a representative of these Foliaceous Lichens. The Fruticose Lichens are distinguished as a third group in which the thallus rises from the ground in the shape of a shrub, whilst the cylindrical, fistular, and ligulate stemlets, which ramify profusely, are only adherent to the substratum by a very small surface at the base. With these are associated the Beard Lichens, which hang down from the bark of old trees in the form of pale, copiously-branched filaments. Lastly, there is a fifth group, the

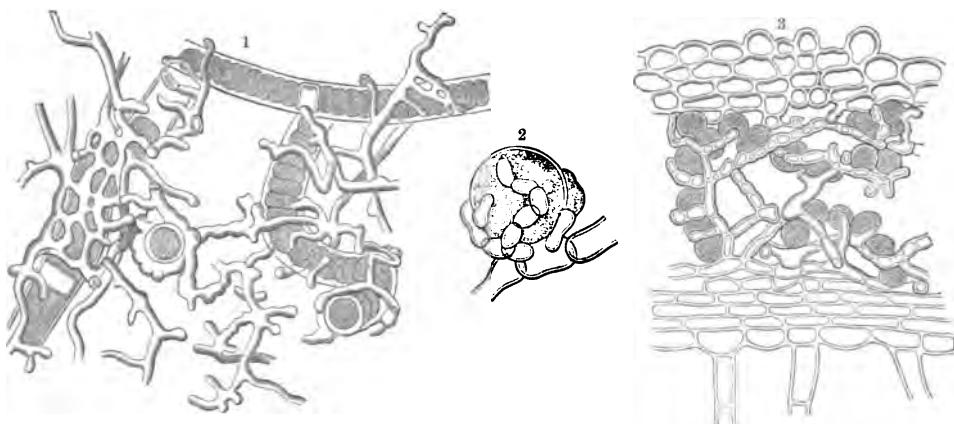


Fig. 58.—Fruticose and Foliaceous Lichens.

<sup>1</sup> *Stereocaulon ramulosum* in conjunction with *Scytonema*;  $\times 650$ . <sup>2</sup> *Cladonia furcata* with *Protococcus*;  $\times 950$   
<sup>3</sup> *Coccocarpia molybdaea*; section,  $\times 650$  (after Bornet).

Gelatinous Lichens, which when moistened look like dark, olive-green, or almost black lumps of wrinkled and wavy jelly or as if composed of variously-divided bands and strips packed together into little cushions.

In the gelatinous expansions last mentioned the algal cells are arranged in moniliform rows and are interwoven with the hyphal filaments of the fungus throughout the entire thickness of the thallus, as in *Collema pulposum* (see fig. 57<sup>2</sup> and 57<sup>3</sup>), or else they form regular ribbon-shaped double rows, interwoven with few hyphae, as in *Ephebe Kernerii* (see fig. 57<sup>1</sup>). In crustaceous, foliaceous, and fruticose lichens, the algal cells constitute a disorderly heap and are crowded together in the middle stratum of the thallus, where they are imbedded between an upper and a lower layer of densely felted hyphal threads, as in *Coccocarpia molybdaea* (fig. 58<sup>3</sup>).

Seeing the wide distribution of lichens it must be assumed that both partners occurring in the lichen-thallus are able to range about with extraordinary ease and latitude. When one observes how patches of the most various lichens are produced in a few years after a landslip on the freshly-broken surfaces of the stones which

have fallen down into the valley beneath, one can only explain the phenomenon by supposing that the algal and fungal cells concerned have been blown together, and that the opportunity has been afforded them on the blocks of stone of contracting a union. Now, so far as regards one of the two partners, viz.: the one devoid of chlorophyll, and known as a fungus—the idea that everywhere in the air spores of fungi are swarming about is so familiar to us that the supposition of an occasional stranding of individual spores, which are being blown about by the wind, upon the moist broken surfaces of stones can encounter no opposition. Respecting those spores in particular which are ejected from the aerial fructifications of lichens, the discussion of their life-history and distribution must of course be reserved for a later section; but it is necessary to make here the one statement that provision exists for the most profuse and distant dissemination of these spores.

Thus, in the case of one of the partners, there is no difficulty in realizing its ubiquity. But when one comes to the *Algæ*, the name at first calls up to mind the green filaments which occupy our pools and ponds, or the brown wracks and red *Florideæ* of the sea-shore, and we ask ourselves how it can be possible for these plants to occur on fractured surfaces of stone, especially on the débris of mountain sides. Indeed, it is certainly not *Algæ* of these kinds that take part in the construction of Lichens. The name *Algæ* is properly only a general name for all *Thallophytes* containing chlorophyll, and it is applied to many small organisms besides those mentioned above, namely, to numbers of *Nostocineæ*, *Scytonemeæ*, *Palmellaceæ*, *Chroolepideæ*, and these are the kinds which fall in with the cells of fungi and form lichens in conjunction with them. Owing to their minute size, they are apt to escape observation, and, in general, only attract attention when myriads of them clothe the bark of trees, cliffs, stones, or earth. In these situations they need but little moisture, and it is not necessary for any of them to live under water like other *algæ*; they become desiccated without sustaining the slightest injury and make their appearance on the substratum occupied by them at the first stage of their development, as powdery coats, and, in this condition being extremely light, are liable to be blown away by a wind of moderate strength, and so distributed over mountain and valley.

That this dissemination is not merely hypothetical but an actual fact has been susceptible of easy proof by the following experiment, made in a mountain-valley in the Tyrol. A plane surface covered with white filter-paper, which was kept moist, was exposed to a south wind; in the course of a few hours numerous particles, like dust, adhered to the paper, and amongst them cell-groups of *Nostocineæ* and others of the above-mentioned *algæ* occurred regularly, in addition to organic fragments of the most various kinds, such as pollen-grains and spores of all sorts of mosses and fungi. All these bodies were deposited in the little depressions on the sheet of paper, and in the same way they rest in the grooves, cavities, and cracks in the surfaces of stone, bark, and old wood-work, where they succeed in reaching a further development as soon as the requisite quantity of water is provided. Now, if at these places the little algal cell-groups meet with hyphæ belonging to the

other potential partner, the latter embrace and enmesh them, as is shown in the above figures, and thus is produced the confederacy called a Lichen. The member destitute of chlorophyll takes up nutriment from the external environment; it possesses, in particular, the property of condensing aqueous vapour, and has, besides, the power of bringing the solid substratum partially into solution by means of excreted substances; it effects adhesion to the substratum, and, in a majority of cases, determines the form and colour of the lichen-thallus as a whole. The second member, whose cells contain chlorophyll, undertakes the task of producing organic matter, under the influence of sunlight, from the materials conveyed to it; by this means it multiplies the number of its cells and increases in volume, whilst, at the same time, it yields to its mate so much as is necessary in order to enable the latter to keep pace with it in growth.

The number of alga which enters into a partnership of this kind is, in any case, much less considerable than that of the fungi, and it must be assumed that one species of alga may unite with the hyphae of different lichen-fungi. The extreme variety, moreover, in the combinations of the two sorts of confederate occurring on a very small area is obvious from the circumstance that it is not rare for half a dozen different species of lichen to spring up side by side on a patch of rock no bigger than one's hand. Whether they all achieve an equally hardy development, or whether some perchance are not crowded out and overgrown by others depends on various external conditions—on the chemical composition of the substratum, and particularly on the conditions of moisture and illumination of the site in question. Lichens are very sensitive in this respect, and the different sides of a single rock often exhibit quite different growths of lichens. A very instructive example of this is afforded by a marble column near the famous castle of Ambras in Tyrol. This column is octagonal, and has been standing in its place for more than two hundred years, with all its sides exposed to wind and weather. Lichens have settled on all the eight faces, and, indeed, are present in such abundance that the stone is quite covered by patches the size of a man's hand. Many of these growths are but poorly developed, and not susceptible of being identified with certainty; but altogether on this column there must be over a dozen different species, the germs of which can only have been brought by winds. These species are, however, by no means uniformly disposed; some prevail on one side, some on another, and a few are confined exclusively to one of the eight faces. Of three species of *Amphiloma*, the one named *A. elegans* is restricted to the warmest side, i.e. the face exposed to the south-west; a second, *Amphiloma murorum*, is to be seen on the upper part of the southern face; whilst *Amphiloma decipiens* occurs on the same face, but only near the ground. On the side with a northern aspect *Endocarpon miniatum* predominates, and on the north-west face *Calopisma citrinum* and *Lecidea* are the prevailing forms.

What thousands of spores and algal cells must have been blown on to this pillar to enable all these combinations to arise! What complex processes must have gone on before the selection of lichens best adapted to each different quarter

of the compass was effected on this little marble column! It is necessary to add, however, that lichens growing on stone, bark, or any situation of the kind do not in all cases owe their original appearance on the substratum to a fresh union of Algae and Fungi, but that there is a second mode of distribution of lichens. This method consists in the transportation by air-currents of already completed social colonies to places often situated at a great distance from the spots where the initial union between Alga and Fungus was contracted. The process is as follows: —in the interior of an old, large, and fully developed lichen-thallus certain groups of cells separate from the rest, each group consisting of one or more green algal cells enmeshed in a dense weft of hyphæ. When a sufficient number of these daughter-associations has been formed the thallus of the parent lichen is ruptured and the little miniature social-groups, which are termed "soredia", come to the surface. To the naked eye a single soredium is only visible as a bright dot, but all together they have the appearance of a mass of powder or meal lying loosely upon the old lichen-thallus. In dry weather this mealy efflorescence is easily blown away with other organic particles. If, then, a soredium thus removed comes to rest in the crack of a rock or on any suitable substratum, the alga and hyphæ composing it continue to develop, and the organism grows into a larger lichen-thallus, which is able to repeat the process just described. In regions where lichens abound, soredia of the kind are found regularly amongst the elements of the organic dust, and occur, indeed, mixed with fungal spores and algal cells, so that it certainly happens not infrequently that two spots close together in the same cranny of stone exhibit both sorts of lichen-growth, the one newly produced by the concurrence and union of algal and fungal cells, the other a daughter-association which has arisen from an old lichen, as a soredium, and is continuing its development.

Another case of symbiosis allied to that of lichens is manifested by certain Cryptogams which live socially together under water and have received the systematic names of *Mastichonema*, *Dasyactis*, *Enactis*, &c. In them also a plant containing chlorophyll, and belonging to the group of Nostocineæ, appears as one member of the partnership; whilst the second is some species of *Leptothrix* or *Hypheothrix*. The green moniliform rows of cells of Nostocineæ are enmeshed and wrapped round by the delicate, filamentous cells devoid of chlorophyll of the *Leptothrix* or *Hypheothrix*; and later, by repeated processes of division, whole colonies of green cell-filaments ensheathed in this manner are produced, which to the naked eye appear as small soft tufts, usually clinging to porous limestone in the spray of waterfalls. In many cases the filaments destitute of chlorophyll rest upon the moderately thickened cell-membranes of the green algae, whilst in other cases they insinuate themselves into the thick cell-membranes, permeate them with their webs, and form in conjunction with them the sheathing envelope.

SYMBIOSIS OF GREEN-LEAVED PHANEROGAMS WITH FUNGAL MYCELIUM  
DESTITUTE OF CHLOROPHYLL.—MONOTROPA.

Another instance of symbiosis is observed to exist between certain flowering plants and mycelia of fungi. The division of labour consists in the fungus-mycelium providing the green-leaved Phanerogam with water and food-stuffs from the ground, whilst receiving in return from its partner such organic compounds as have been produced in the green leaves.

The union of the two partners always takes place underground, the absorbent roots of the Phanerogams being woven over by the filaments of a mycelium. The first root that emerges from the germinating seed of the phanerogamic plant destined to take part in the association descends into the mould still free from hyphæ; but the lateral roots and, to a still greater extent, the further ramifications, become entangled by the mycelial filaments already existing in the mould or proceeding from spore-germs buried there. Thenceforward the connection continues until death. As the root grows onward, the mycelium grows with it, accompanying it like a shadow whatever its course, whether the root descends vertically or obliquely, or runs horizontally, or re-ascends, as is sometimes necessary when it happens to be turned aside by a stone. The ultimate ramifications of roots of trees a hundred years old, and the suction-roots of year-old seedlings, are woven over by mycelial filaments in precisely the same manner. These mycelial filaments are always in sinuous curves and intertwined in various ways, so that they form a felt-like tissue, which looks, in transverse section, delusively like a parenchyma. As regards colour the cell-filaments are mostly brown, sometimes they are almost black, and it is rare for them to be colourless. The epidermis of many roots is covered as if by a spider's web, whilst the hyphæ form a complex tangle of bundles and strands broken here and there by open meshes through which the root is visible. In other cases an evenly woven but very thin layer is wrapped round the root; and in others, again, the fungus-mantle forms a thick layer which envelops uniformly the entire root (see fig. 59). Here and there the hyphæ insinuate themselves also inside the walls of the epidermal cells, and the latter are permeated by an extremely fine small-meshed mycelial net (see fig. 59<sup>3</sup>). Externally the mantle is either fairly smooth and clearly marked off from the environment, or else single hyphæ and bundles of hyphæ proceed from it and thread their way through the earth. When these branching hyphæ are pretty equal in length they look very much like ordinary root-hairs. And they not only resemble them, but assume the function of root-hairs. The epidermal cells of the root, which would in an ordinary way act as absorption-cells, being inclosed in the mycelial mantle cannot exercise this function, and have relegated the business of sucking in liquid from the ground to the mycelium. The latter undoubtedly acts as an absorptive apparatus for the partner on whose roots it has established itself; and the water in the soil, together with all the mineral salts and other compounds

dissolved in that water, are caused by the mycelial mantle to pass from the surrounding ground into the epidermal cells of the root in question, and thence onward, ascending into axis, branches, and foliage.

Thus the fungus-mycelium not only inflicts no injury on the green-leaved plant by entering into connection with its roots, but confers a positive benefit, and it is even questionable whether a number of green-leaved plants could flourish at all without the assistance of mycelia. The experience gained in the cultivation of those trees, shrubs, and herbs, which exhibit mycelial mantles on their roots, does not, at any rate, lead to that conclusion. Every gardener knows that attempts to rear the various species of winter-green, the bog-whortleberry, broom, heath, bilberries, cranberries, rhododendrons, the spurge-laurel, and even the silver-fir and

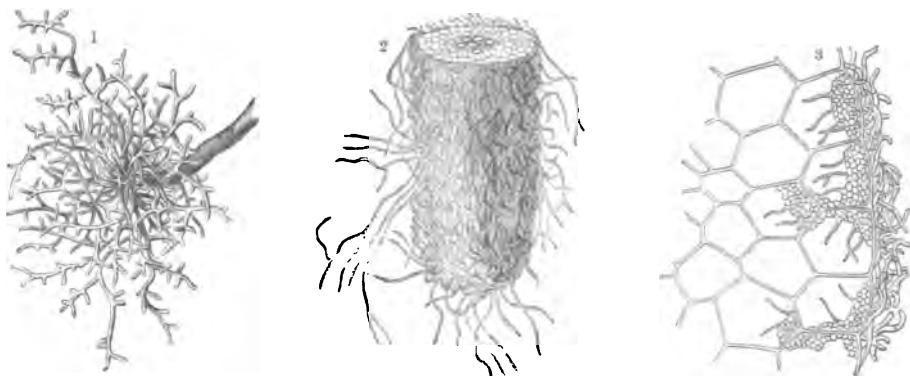


Fig. 59.

<sup>1</sup> Roots of the White Poplar with mycelial mantle. <sup>2</sup> Tip of a root of the Beech with closely adherent mycelial mantle;  $\times 100$  (after Frank). <sup>3</sup> Section through a piece of root of the White Poplar with the mycelium entering into the external cells;  $\times 480$ .

the beech, in ordinary garden soil are not attended with uniform success. Therefore, as is well known, soil consisting of vegetable mould from the top layer of earth in woods or on heath is chosen for the cultivation of species of the genera *Erica*, *Daphne*, and *Rhododendron*. But it is not even every kind of forest- or heath-mould that can be made use of. When earth of that nature has been quite dry for a long time it is no longer fit for this purpose. On the other hand, it is known that the above-mentioned plants should be transplanted from their forest-home with the soil still clinging to the roots, and it is also laid down as an axiom that the roots of these plants should not be exposed and should be cut as little as possible. The following reasons account for all this. Firstly, fresh earth from a heath, or mould recently dug from the ground in a wood, contains the mycelia still alive, whereas in dry humus they are already dead; secondly, the mycelia woven round the roots are transferred together with the balls of earthy matter suspended to them into the garden; and, lastly, any considerable clipping of the roots would remove the ultimate ramifications which are furnished with the absorbent mycelial mantle.

The failure of all attempts to propagate the oak, the beech, heath, rhododendron, winter-green, broom, or spurge-laurel, by slips or cuttings, if the shoot which is cut

off and used for the purpose is put into pure sand, is explicable in the same way. Limes, roses, ivy, and pinks, the roots of which possess no mycelial mantle, are notoriously propagated very easily by putting branches cut from them into damp sand. Rootlets are at once produced on those parts of the branches which are buried in the sand, and their absorption-cells carry on the task of taking up nutriment from the ground. But though cuttings of oak, rhododendron, winter-green, bog-whortleberry, and broom strike root, no progress in their development is to be observed, because the superficial cells of the rootlets, in these cases, have not the power of absorbing food when they are not associated with a mycelium. It is only when the slips from these plants are put into sand with a rich admixture of humus, the latter having just been taken from a wood or heath and containing the germs of mycelia, that some few are successfully brought to further development. The result is even then often not assured, and the cuttings of several of the plants enumerated die even in sand mixed with humus before they have produced rootlets.

Seeing also that the result of attempts to rear seedlings of the beech and the fir in so-called nutrient solutions, where there could be no question of any union with a mycelium, has been that the plantlets dragged on a miserable vegetative existence for a short time and ultimately died, we have good grounds for assuming that the envelope of mycelial filaments is indispensable for the Phanerogams in question, and that the prosperity of both is only assured when they are in social alliance.

The facts ascertained in cases of analogous relationship lead one to expect that the fungus-mycelia also derive some advantage from the flowering-plants, the roots of which they clothe, and to which they render the service of acting as absorption-cells. The benefit in question is undoubtedly the same as that derived by the hyphae of a lichen-thallus from the enwoven green cells. The mycelial mantles withdraw from the roots of the Phanerogams the organic compounds which have been elaborated by the green leaves in the sunshine above-ground, and which are conducted thence to all growing parts, that is to say, downwards as well as in other directions, to the tips of the swelling and elongating roots. According to this, therefore, the division of labour between the members of the alliance for joint nutrition consists in the mycelium supplying the green-leaved plant with materials from the ground, and the green-leaved plant supplying the mycelium with substances which have been worked up above-ground in the sunlight.

The range of species which live in a social union such as is here described is certainly very large. All Pyrolaceæ, Vaccineæ, and Arbuteæ, most, if not all, Ericaceæ, Rhododendrons, Daphnoideæ, and species of *Empetrum*, *Epacris*, and *Genista*, a great number of Conifers, and apparently all the Cupuliferæ as well as several Willows and Poplars are dependent for nutrition on the assistance of mycelia. We find, too, that this condition recurs in every zone and in every region. The roots of the *Arbutus* on the shores of the Mediterranean are equipped with a mycelial mantle in precisely the same manner as those of the low-growing Whortleberry of the High Alps.

Special importance is given to the social life by the fact that the chief species of Phanerogams participating in it are of gregarious growth and cover whole tracts of country, forming boundless heaths and measureless forests, as, for instance, the various heaths, the oak, the beech, the fir, and the poplar. The conception of this subterranean life affecting every moorland and vast timbered tract is one full of wonder and interest.

We can now see why it is that the ground in woods is the abode of such a profusion of fungi. No doubt some of these fungi draw their nutriment exclusively from the store of dead plant-organs accumulated there; but others, as certainly, are in social connection with the living roots of green-leaved plants. It is true we cannot yet state precisely what are the species of fungi which contract this sort of union, or whether generally a definite elective affinity exists between certain fungi and certain green-leaved plants. There is much in favour of this supposition in a few cases: but, on the other hand, it is very unlikely that each of the various Phanerogams occupying a limited area of ground in a pine-forest, where a few square meters of earth contain so many tangled roots belonging to pines, spurge laurels, bilberries, cranberries, heath, and winter-green, that they can only be separated with difficulty, should select from the great host of fungi growing in the forest a different partner. In instances of this kind it seems just to suppose that the mycelium of one and the same species of fungus enters simultaneously into connection with all or several of the plants growing close together; it is similarly probable that the mycelia of different species of fungi render to one and the same flowering-plant the service of absorption according to the locality in which it occurs. This surmise is supported by the fact that when certain species, brought from distant parts and regularly exhibiting mycelial mantles on the ends of their roots, are reared in our gardens and greenhouses from seed, they unite in these abodes with fungus-mycelia, which certainly do not exist in the regions where the Phanerogams in question grow wild. Thus, for instance, the roots of the Japanese tree, *Sophora Japonica*, and those of the Epacridæ of Australia, are found in European gardens in social union with fungi, which with us are native, but which certainly do not occur in Japan or Australia; and it is therefore scarcely open to doubt that the *Sophora Japonica*, to take one example, associates itself with different fungi in different regions.

Now that the symbiosis of fungi devoid of chlorophyll with green-leaved Phanerogams has been discussed, we are for the first time in a position to deal with that most remarkable of all cases of food-absorption wherein the subterranean roots of a flowering-plant are completely wrapped in a mycelial mantle, whilst the parts which shoot up above ground bear no green leaves, and, in general, possess no trace of chlorophyll. Such is the case of *Monotropa*, the various species of which are intimately allied in the structure of flowers and fruit with the Primrose and Winter-green, and are met with scattered everywhere in shady woods. Their stems, which are from 10 to 20 centimeters in height and emerge from the mould of the forest-ground in summer time, are thick, fleshy, succulent, and profusely beset with

membranous and transparent scales, and the extremity of each is bent back like a hook. The cylindrical flowers are developed at the top of the stem with their open ends turned to the ground, and are half-covered by the scales. Everything about this plant (stem, leaf-scales, and flowers) is of a pale waxen-yellow colour, and the general impression it produces is much more that of a Toothwort, or one of the colourless forest orchids, than of a species of primula or winter-green. Towards autumn, when ripe fruits have been produced from the flowers, the hitherto drooping extremity of the stem lifts itself into an upright position, whilst the entire aerial portion of the plant turns brown and dries up. Every disturbance caused by the wind, however slight, shakes out of the spherical fruits many thousands of tiny seeds as fine as dust, which, like the winter-green seeds, consist of only a few cells, and do not admit of the recognition of any differentiated embryo within them. Moreover, underground, the rhizomes, from which the small group of pale stems have arisen in summer, continue to live through the winter, and a number of new buds are developed on them. On digging down to the hibernating plant and removing the mould which conceals it, one finds at a depth of from 10 to 40 centimeters bodies like coral-stems consisting of dense masses of roots crowded together and ramifying multifariously. All the root-branches are short, thick, fleshy, and brittle, and are matted together to form turf-like masses, which are not infrequently interwoven with the rootlets of pines, firs, and beeches, and have all their interstices filled with humus. Each rootlet is enveloped, right up to the growing apex, in a thick mycelial mantle. The hyphal filaments of this mycelium do not penetrate into the tissue of the root of *Monotropa*, nor do they send any haustoria into the superficial cells of these roots. The hyphae and the epidermal cells of the root are, however, in such close and continuous contact that sections exhibit a complete continuity of the tissues.

*Monotropa* is therefore only able to withdraw nutriment from the hyphal weft of the mycelium so far as its subterranean parts are concerned, and, seeing that it is quite destitute of chlorophyll, and its aerial stem and leaves display no trace of stomata, the possibility of creating organic matter and of adding in general to its substance by means of its aerial parts is excluded. It therefore receives all the materials of which it is constructed from the mycelium of the fungus, whilst it is not in a position to render anything in return to this mycelium that it has not previously derived from the latter. If the mycelium subsequently withdraws any materials whatever from the still living or decaying *Monotropa*, the process is only one of restitution and not of exchange. Thus, in this case, there can be no talk of reciprocity in the processes of nutrition or division of labour such as occurs when there is symbiosis. The *Monotropa* grows in height and in circumference entirely at the expense of the mycelium in which it is imbedded, so that we have here the remarkable phenomenon of a Phanerogam parasitic in the mycelium of a Fungus. We so often come across the converse process in our experience that we cannot easily familiarize ourselves with the idea of a flowering-plant draining the mycelium of a fungus of nutriment: nevertheless there is scarcely any other inter-

pretation possible in this case, for all the other hypotheses,—such as that *Monotropa* enters into connection with the roots of trees, or that it is parasitic in the first stages of development, but subsequently detaches itself from its host and becomes a saprophyte,—rest on inaccurate observations, and have long been disproved. As a parasite *Monotropa* ought to have been discussed at the same time as others in earlier pages, but it was not without intention that the description of this plant was reserved for this place, for it would have been difficult to state and explain the method of nutrition exhibited by it before some previous knowledge of the curious phenomena of union of the mycelia of fungi with the roots of green-leaved Phanerogams had been acquired.

#### ANIMALS AND PLANTS CONSIDERED AS A GREAT SYMBIOTIC COMMUNITY.

If we look back at the cases of symbiosis already discussed and inquire what is their value, we find it consists in an integration of the functions of plants possessing chlorophyll and plants not possessing it. The reciprocity here implied is, however, at bottom, but a copy of the complementary interaction of plants and animals which takes place on a grand scale in the organic world. The associated plant, destitute of chlorophyll, in which capacity fungi are always the organisms concerned, really plays the same part in the social life as is taken by animals in the great economy of nature, and this is in harmony with the fact that in other respects as well fungi exhibit so many similarities to animals that in many instances one looks in vain for a line of division to separate them from animal organisms. Hence there is no need for surprise when cases come under observation wherein a quite unmistakably animal organism enters, instead of a fungus, as one of the partners in a symbiotic community. Certain Radiolariaæ have small yellowish spots upon them, which were formerly held to be pigment-cells, but have proved to be little algæ, with cells furnished with true chlorophyll. Similar properties are exhibited by the fresh-water polyp, *Hydra*, and by the marine sea-anemones. Small algæ occur in social union with these also in the shape of cells with membranes made of cellulose and containing chlorophyll and starch-grains in their protoplasmic bodies. These algæ are in no wise injurious to the animals with which they are associated; on the contrary, their presence is beneficial, their partners reaping an advantage from the fact that the green constituents split up carbonic acid under the influence of the sun's rays, and in so doing liberate oxygen which may be again taken in by the animals direct, and serve a useful purpose in their respiration and all the processes connected therewith. Conversely, the algæ, in association with the animal's body, will derive a further advantage from the latter, inasmuch as it receives at first hand the carbonic acid exhaled by the animal in breathing. The small algæ living socially with animals cannot be reckoned as parasites in any case, nor can the animals be looked upon as parasites of the algæ, but we have here the phenomenon of mutual assistance and of a bond serving for the benefit of both

parties, precisely similar to that noticed in the case of lichens and in the others which have been described above.

Several of the liverworts which live as epiphytes on the bark of trees exhibit on the under surface of their leaflets (which are inserted on the stem in two rows, and are pressed flat against the bark) little auricular structures, and in species of the genus *Frullania*, these take the form of definite hoods or pitchers. The rain that trickles down the trunks of the trees, washing the bark and wetting the liverworts in its course, fills the hooded receptacles referred to with water, and is retained longer in these protected cavities than anywhere else, if a period of drought ensues and the liverwort becomes dry again. Now these cowls are the abode of tiny rotifers (*Callidina symbiotica* and *C. Leitgebii*), which live on the organic dust brought thither with the water. In return for the peaceful home thus afforded them in the hooded chambers of the leaves, the rotifers supply the liverworts in question with nitrogenous food. For as such must serve the matter excreted by the rotifers in the interior of the cowls. Without the intervention of the rotifers, the living organisms (Infusoria, Nostocineæ, and spores) contained in the water could not be converted into food by the liverworts, whereas the liquid manure arising from the Infusoria, Nostocineæ, and spores, digested in the bodies of the rotifers, contains highly nitrogenous compounds, which are of great value to the liverworts in question, as indeed they are to all epiphytes living on the bark of trees. It stands to reason that the symbiotic liverworts and rotifers derive also a mutual advantage from the fact that the oxygen set free by the former comes into the possession of the rotifers and the carbonic acid emitted by the rotifers into that of the liverworts by the most direct method.

Moreover, these cases of partnerships further remind us of other analogous relations existing between plants and animals, which it is necessary to refer to now, although they cannot be treated in detail till later on. A great number of flowering-plants excrete honey into their flowers, and so attract flying insects to them, which supply themselves plentifully, and in their turn render to the plants they visit the service of transferring the pollen from flower to flower, thus making possible the development of fruits and fertile seeds. Certain small moths which visit the flowers of *Yucca* bring the pollen to the stigmas, and force it into the stigmatic orifices in order that mature fruits and seeds may be produced from the rudimentary fruits, a result which is indeed a matter of vital importance to these moths. For the moths lay their eggs in the carpels of *Yucca*, and from the eggs larvæ are developed which live exclusively on the seeds of this plant. If the *Yucca* were not fertilized, and did not develop any fruit, the larvæ would die of hunger. A similar phenomenon occurs in many other cases of the kind, where both plant and animal reap some benefit. On the other hand, in the formation of galls, which are produced by animals laying their eggs in particular parts of plants, the advantage (with few exceptions) is all on the side of the animals, and these gall-structures might most justly be placed by the side of parasitic structures.

It is obvious from all this that such of the mutual relations of plants and of

their relations to animals as are occasioned by the endeavour to acquire nutriment are extremely various and often linked together and complicated or deranged by one another in the most curious manner. Cases occur of a particular plant being socially connected with another, and at the same time also beset by vegetable and animal parasites. The absorption-roots of the Black Poplar are covered with a dense mycelial mantle, so that this tree is associated for purposes of nutrition with the fungus to which the mycelium belongs. Such parts of the roots of the Black Poplar as are left free from the mycelium are fastened upon by suckers sent forth by Toothwort plants, which withdraw from the roots the juices absorbed by the latter from the earth through the instrumentality of the mycelial mantles clothing them. Meantime, in the cavities in the leaves of the Toothwort various small animals are caught and made use of as nitrogenous food. Again, the poplar-tree bears Mistletoe on its boughs, and its presence there is due to the missel-thrush. The thrush takes the Mistletoe-berries for food, and, in return, renders the plant the service of dispersing the seeds and establishing them on other trees. The parasitic Mistletoe takes its liquid nutriment from the wood of the poplar-tree; but, on the other hand, its own stems are covered with lichens, and these lichens are themselves a symbiotic community of algae and fungi. Within the wood of the poplar-stems spread the mycelia of certain Basidiomycetes (*Panus conchatus* and *Polyporus populinus*), whilst the foliage-leaves are covered with a little orange-coloured fungus, *Melampsora populina*. In addition, no less than three gall-creating species of *Pemphigus* live on the leaves and branches of the Poplar, and a number of beetles and butterflies are nourished by them. Certain lichens, mosses, and liverworts regularly settle on the bark of old trunks, and included amongst these may be the species of liverwort which is inhabited by rotifers. If all the plants and animals which live upon the poplar-tree, within it or in association with it, are counted, the number turns out to be not much fewer than fifty.

---

## 7. CHANGES IN THE SOIL INCIDENT TO THE NUTRITION OF PLANTS.

Solution, displacement, and accumulation of particular mineral constituents of the soil owing to the action of living plants.—Accumulation and decomposition of dead plants.—Mechanical changes effected in the soil by plants.

### SOLUTION, DISPLACEMENT, AND ACCUMULATION OF PARTICULAR MINERAL CONSTITUENTS OF THE SOIL RESULTING FROM THE ACTION OF PLANTS.

Reference was made in the preceding section to a marble pillar on the faces of which a dozen different lichens have settled in the course of centuries. I again introduce to the reader's notice this unobtrusive monument in order to demonstrate in its case the changes to which stone is subjected by the plants clinging to it or nestling in its crevices. It may be premised, as a matter of course, that when the marble column was erected two hundred years ago the eight sides were polished, and presented perfectly even surfaces. But what is its appearance to-day? The whole is rough and uneven; in parts it is as though corroded, and there are little pits clustered together in places. The idea might arise that depressions have been formed in course of time by the impact of drops of rain, but nearer inspection shows that there can be no question that the inequalities have been produced in this way; on the contrary, it is by the influence of the lichens adherent to the stone. Especially on the two sides of the pillar facing south and south-west, one sees clearly how each pit corresponds exactly in size to a species of grey lichen there ensconced, and how this lichen, as it continues to grow and extends radially, corrodes and etches the marble it touches in ever-widening circles. The expression "to etch" may here be taken literally, for there is no doubt that the process, the result of which is manifested in the formation of little pits, is mainly caused by the excretion of carbonic acid from the lichen's hyphæ, whereby the calcium carbonate is converted into bicarbonate. The latter, being soluble in water, is, in part, taken up by the lichen as nutriment, whilst part is washed away by the rain.

In addition to this chemical action, the hyphal filaments exercise also a purely mechanical influence. A growing hypha penetrates wherever the merest particle of carbonate of lime has been dissolved and accomplishes regular mining operations at the spot. Projecting particles of the carbonate not yet dissolved are separated by mechanical pressure from the main mass; and at the places in question where a lichen is in a state of energetic growth, tiny loose rhombohedral fragments of the lime are to be seen, which are washed away by the next shower or else carried off as dust by the wind. The same process as that which may be so clearly traced on the marble pillar at Ambras takes place, of course, also on the limestone that has not been carved or polished, in every locality where lichens exist at all. We notice it in the case of other kinds of stone as well—in dolomite, felspar, and even in pure quartz rock—for even quartz is not able to withstand the long-continued action of

carbonic acid and the mechanical operations above referred to in the performance of which the hyphæ act like levers. Some of the powerful iron bands belonging to the great suspension bridge across the Danube at Budapest afford us the opportunity of observing the mining operations of lichens on a substratum of pure iron. Of course in these cases the decomposition and solution initiated by the carbonic acid varies according to the nature of the substratum; the result is, however, invariably the same; there is always a loss of substance on the part of the substratum, and a part of the dissolved matter is always taken up by the adherent plant, whilst another part is carried away either in solution or mechanically by wind or rain.

Mosses act in precisely the same manner as lichens. If a tuft of *Grimmia apocarpa* is lifted away from the side of a block of limestone, it becomes evident that in the neighbourhood of the place where all the stemlets of the little moss-colony meet, the underlying stone is threaded through and through, and rendered friable. There lie the rhizoids imbedded between isolated particles of lime, which are as fine as dust, and have been disintegrated by the chemical and mechanical activity of the organs in question. At spots where plants of *Grimmia* have died, the limestone always exhibits an obvious loss of substance in the form of unevenly corroded depressions.

The fact that the roots of Phanerogams also alter the subjacent stone in a similar manner may be proved by the following experiment. A polished slab of marble is covered with a layer of sand, and seeds of plants caused to germinate in this sand. The roots of the seedlings as they grow downwards come almost immediately upon the marble slab, and, turning round, creep onward in close contact with the stone. After a short time the parts of the slab against which the roots are pressed become rough as though they had been etched; a solution of individual particles of the carbonate of lime takes place under the influence of the acid juice saturating the cell-walls of the root's cells, and this circumstance reveals itself to the naked eye as a roughness which is readily perceptible.

Whereas the loss of substance affecting the solid substratum of plants may thus be at once detected by sight, the removal of constituents of the air and of water eludes direct observation. The ingredients withdrawn by plants are instantly replaced in water and still more in the air by influx from the environment, and obviously no holes or pits are the outcome as in the case of a surface of limestone rock.

In the discussions that follow it is important to retain the conception that in the process of vegetable nutrition certain substances may undergo local displacement, accumulation, and aggregation, and temporary consignment to a state of quiescence. Ingredients of the earth's crust are borne upwards into atmospheric regions, and constituent parts of the air are carried deep down into the ground. Lime, potash, silicic acid, iron, &c., pass from disintegrated rocks into the realms above ground—into stems and leaves, and to the tops of the highest trees, whilst carbon and nitrogen pass from the aerial shoots and from the foliage spread out in the sunshine into the deepest shafts which the roots have bored for themselves in

the ground. If one were to mark out the space of ground from which the lime, potash, and other nutrient salts used in the construction of a birch-tree were derived, its bulk would certainly be found to be much larger than that of the birch; and, if we were to try to estimate the volume of air through which the carbon, which has been converted into organic compounds in the tree, was previously distributed in the form of carbon dioxide, it would turn out to exceed the volume of the birch a thousandfold. In this sense, every plant may justly be considered as an accumulator of those substances which serve for its nutriment. Every plant continues, so long as it lives, to store them up in ever-increasing quantities in its own body, and in the case of long-lived plants there is thus collected ultimately quite a considerable quantity. When the life of an accumulator of the kind is extinguished, those materials which were taken from the atmosphere are able to return into the atmosphere; but such mineral food as has been derived from the ground and lifted into the upper parts of the plant—particularly those above the ground—and has there been amassed in a confined space, does not return to its original place. A dead tree breaks down on the first provocation, and the trunk lies on the ground and rots. Such part of its substance as can pass into the atmosphere in gaseous form escapes; but the salts accumulated within it, which it raised from deep under ground during its lifetime, are retained by the surface-layers of the soil. Even though some of them are washed out of the trunk by the lixiviating action of rain-water, the superficial layers of earth operate as a filter, and do not allow any part to return to the underlying strata. So, too, the nutrient salts which reach the foliage of plants are added to the top layers of the soil; for fallen leaves go through much the same process as the trunk which is broken by storms and undergoes decay as it lies prostrate upon the ground.

Thus, wherever men do not interfere by clearing away the accumulative agents in question, *i.e.* plants; where there is no removal of the haulms of cereals from fields, or of mown grass and herbs from meadows to serve as hay, or of timber from the forest—wherever, in a word, the vegetable world is left to itself and the natural progress of evolution is not frustrated by any disturbing element—the food-salts which have been amassed will accumulate in the uppermost layers of the earth. Moreover, seeing that, as has been already pointed out, every plant has the power of possessing itself of substances of value to it, even when they are only present in the environment of the roots in scarcely appreciable quantities, it is possible for the top layers of soil to contain a considerable amount of a substance which only occurs in the subjacent rock in such small measure as to be detected with difficulty. The percentage of lime yielded by the subsoil on the Blöckenstein, a granitic mountain 1383 meters high, on the borders of Bavaria and Upper Austria, was 2·7, whilst that of the top layer was 19·7; the percentage on Mount Lusen, situated to the north of the Blöckenstein, was 1·9 for the subsoil and 8·6 for the superficial layer. When one considers that fresh plants strike root in the ground near the surface and these again act as accumulators, and remembers in addition that snails make their appearance in abundance wherever vegetable food containing

lime is to be found, that these snails again are to be reckoned as accumulators, and that their shells, which consist almost entirely of lime, remain after the animals' deaths in the top layer of soil, it is not surprising to find that the earth-mould on a granite plateau contains a proportion of lime not much less than that yielded by mould resting on argillaceous limestone.

Still more striking than the influence of rock plants and land plants in transposing and accumulating lime is the agency of hydrophytes in causing the same results. In the trickling springs of mountainous regions as well as in the standing pools of level country and no less in the depths of the sea, plants occur which obtain part of the carbonic acid they require by the decomposition of the bicarbonate of lime dissolved in the surrounding water. The monocarbonate of lime, which is insoluble in water, is then precipitated in the form of incrustations upon the leaves and stems of the plants in question. Many of these hydrophytes take up carbonate of lime into the substance of their cell-membranes; and in other cases both phenomena occur, that is to say, not only are they incrusted externally with calcium carbonate, but the cell-walls are also thoroughly impregnated by the same salt. In the streams arising from springs loaded with bicarbonate of lime in solution derived from the heart of a mountain, a number of mosses regularly occur—*Gymnostomum curvirostre*, *Trichostomum tophaceum*, *Hypnum falcatum*, and others besides. These mosses and also several species of Nostocineæ belonging to the genera *Dasyactis* and *Euactis* become completely incrusted with lime, in the manner referred to, but go on growing at the apical end as the older and lower parts imbedded in lime die off. In consequence, the bed of the stream itself becomes calcified and elevated, and, in course of time, banks of calcareous tufa are formed, which may attain to considerable dimensions. Banks raised in this manner are known which are no less than 16 meters in height; to construct them mosses must have worked for more than 2000 years.

Numerous Stoneworts (species of *Chara* or *Nitella*), the Water-milfoil and Hornwort (*Myriophyllum* and *Ceratophyllum*), Water-crowfoots (*Ranunculus divaricatus* and *R. aquatilis*), and more especially many Pond-weeds (*Potamogeton*), which grow in continuous masses in still, inland waters, incrust their delicate stems and leaves with lime during the summer, but in autumn shrink away, that is to say, their stems and leaves fall and decay, leaving scarcely any trace of the mass of vegetation till the advent of the following spring. The calcareous deposits, however, are preserved, and, sinking to the bottom of the water where the incrusted plants lived, form a layer which year by year increases in thickness. Anyone who undertakes the investigation of the sequestered wastes of water in the shallow lakes of lowland districts will be convinced of the magnitude of the scale on which this kind of accumulation must take place. As one's boat glides over places where there is a luxuriant growth of the lime-incrusted *Chara rudis* and *C. ceratophylla*, there is a crepitating sound in the water like the snapping of dry sticks of birch-wood. Great numbers of stoneworts are fractured by the boat as it strikes against them, and if one takes hold of the fragments they feel like a heap of brittle glass.

fibres. What a quantity of carbonate of lime must be deposited yearly at the bottom of these lakes and ponds! Amongst pond-weeds, *Potamogeton lucens*, in particular, clothes its large shining leaves with a very stout, uniform crust, which drops off in scales as the plant dries, the weight of which can be exactly determined in the case of each separate leaf. The result of careful weighing showed that a single leaf equal in weight to 0·492 grm. was covered with a calcareous crust weighing 1·040 grm. Now, supposing one shoot of this pond-weed, having five leaves, and covering an area of 1 square decimeter, decays in the autumn, and lets its lime sink to the bottom of the pond, the approximate weight of lime deposited each year on a square decimeter of the ground at the bottom is 5 grms., and, if this process is repeated every year, a layer is deposited in ten years which weighs 50 grms., and consists of calcium carbonate and traces of iron, manganese, and silicic acid.<sup>1</sup>

There is no doubt that it is possible for calcareous strata of great depth to be produced in this way in fresh water. That also in times past lacustrine deposits of lime have had a similar origin is inferred from the fact that the spore-fruits of stoneworts (*Characeæ*) and the nutlets of pond-weeds have been found over and over again inclosed in these formations of lime. Calcareous deposits originating in this manner are, at present at least, less frequent in the sea. Still, the *Acetabulariæ* undergo similar changes there, and may be the cause of an elevation of the sea bottom and of an accumulation of lime. On the other hand, in the sea, the *Lithothamnia* and *Corallinas* play a predominant part, and form—just like true corals, and often indeed in conjunction with these and other marine animals—lime reefs of great magnitude.

The agency of plants may occasion accumulations of iron hydroxide, silicic acid, and salts of potassium and sodium at particular places besides lime. The formation of meadow iron-ore, spring iron-ore, and bog iron-ore, the construction of tripoli, agate, and flint, by the conglomeration of siliceous-coated Diatomaceæ, and the accumulation of potassium and sodium salts in the superficial strata of salt steppes are processes which take place essentially in the same manner as the piling up of carbonate of lime, although upon a more modest scale.

The question now arises, why it is that the substances which are stored in preponderant quantities in the vegetable frame, which are the main constituents of the living part of plants, and represent the alpha and omega of plant life, are not preserved as well as the mineral food-salts in question. Why do not carbon and nitrogen, materials so eagerly appropriated by the living plant, compounded by it with the elements of water, secured in some measure in organic compounds, and constituting the fundamental mass of the vegetable structure, remain behind in the same condition after the death of the plant? When autumn comes and the lime-laden pond-weed dies, only the calcareous crust falls to the ground, and, at the bottom of the pond, enters upon a period of quiescence. The tissue of the plant

<sup>1</sup>In the case investigated 96 per cent calcium carbonate, 0·28 per cent iron oxide, 1·51 manganese oxide, and 1·51 per cent silicic acid; the last, from the Diatomaceæ, settled on the calcareous crust.

itself—all its carbohydrates and albuminoid compounds—cannot remain dormant, but are split up without delay into those simpler compounds of which they were compounded in the summer; and, by the following spring there is nothing more to be seen of any of the pond-weed's stems and leaves. Certainly this is only to such a conspicuous extent true of plants living under water; dead plants buried in earth or exposed to the atmosphere are resolved less rapidly, and under certain circumstances deposits of organic remains on limited areas are preserved even almost unaltered through boundless ages.

Let us try to obtain a somewhat closer knowledge of these various degrees of preservation. Thoroughly dried wood, leaves, and fruit, if protected from all but transient moisture, are capable of being preserved unaltered for long periods of time. When wood is exposed in a dry place to the sun, it turns brown, and in the course of years becomes quite black outside, the most superficial layers being regularly carbonized, as may be seen particularly well in the case of woodwork situated under the projecting roofs of old mountain chalets. This wood exhibits no sign of crumbling, mouldering, or rotting. In the dry chambers of old Egyptian graves fruits, foliage, and flowers have been found which were laid by the side of the corpses 3000 years ago, and they had not undergone a greater change than if they had been dried but a few days. Even the colours of flowers of the Larkspur, the Safflower, and other plants of the kind, were still to be seen, and the separate stamens in Poppy flowers were in a state of complete preservation. Dryness therefore may be looked upon *par excellence* as one of the preventives of the decomposition of organic matter.

The same result as is secured by dryness in the cases cited is brought about in the ground of moors by humous acids. The dead plants saturated with these acids are not resolved into carbonic acid, water and ammonia, but preserve their form and weight almost unaltered, and are converted into peat. Above the mass of peat new generations of plants continue to spring up and produce ever fresh organic matter, which, in its turn, becomes peat, and is added to the mass beneath, so that gradually a very deep bed of organic matter may be accumulated in this manner. In the low country lying between East Friesland and the Hümmeling, from the river Hunte to the marshes on the Dollart, there is a stretch of nearly 3000 sq. kilometers covered with a layer of peat which has an average depth of 10 meters.

Of minor importance is the preservation of dead plants and parts of plants in snow and ice. The leaves, twigs, and seeds, which are carried by the wind on to the snow-fields of the high mountains, remain there a long time almost without alteration in respect of form or size; they only turn brown under the influence of the intense sunlight, and at last become quite black as though they were carbonized, which, in fact, they are. So also such insects as meet their death on the snow-fields are converted there into a black, cindery mass. Indeed, even all the minutest organic fragments lying on a glacier become carbonized, and this explains the fact that the so-called cryokone, or snow-dust, which we have already had occasion to allude to, has a graphitic appearance.

Dead leaves, haulms, branches, and tree-trunks, when they rest upon damp ground, as also lifeless roots, rhizomes, bulbs, and tubers, buried in moist earth, pass into a state of putrefaction, provided that their temperature does not fall below freezing-point, that is to say, they are resolved into carbonic acid, water, and ammonia, the rapidity of the process varying directly as the supply of water and the degree of temperature to which the dead matter is exposed, and inversely as the quantity of compounds of humous acid present. If more dead fragments of plants accumulate within a particular interval of time on one spot than decay, a formation of vegetable mould takes place there; on the other hand, the ground remains destitute of humus when the entire accretion of organic matter is quickly decomposed as soon as it is dead. The general fact turns out to be that the decomposition of organic bodies is prevented, or at least limited, by a dry condition, and is promoted by moisture, and that it can only be prevented in moist surroundings by the presence of large quantities of humous acids, or by the temperature being low enough to turn water into ice.

This result directs attention to those inconceivably small animate beings, which, as has been proved by experience, are arrested in their activity by scarcity of water and are killed by the antiseptic substances referred to. That they are the cause of the resolution of dead plants is corroborated by the facts that they are always present where vegetable putrefaction is in progress, and that, on the other hand, decomposition can be prevented by rendering the access of these minute organisms impossible. First in importance in this respect of course are bacteria, the causal connection of which with processes of dissolution, and especially with those decompositions, which are known by the name of putrefaction, is established. Of these bacteria, *Bacterium Termo*, and several micrococci, bacilli, vibriones, and spirilla, are the commonest. Their multiplication and the withdrawal for this purpose of substances from dead plants cause a splitting up of the organic compounds in the latter. The albuminoid compounds are first of all peptonized; next, tyrosin, leucin, volatile fatty acids, ammonia, carbon-dioxide, sulphuretted hydrogen, and water are formed, this stage of the process being accompanied by the evolution of an offensive odour of decomposition, and later, nitrous and nitric acids are produced by further oxidation. The carbohydrates, too, chiefly cellulose and starch, are split up, and the products of this analysis, in so far as they are not used up by the bacteria for their growth and reproduction, pass in a gaseous condition into the atmosphere, or into the water surrounding the dead plants. Moreover, the bacteria themselves do not remain at the spots where they have been battening on vegetable matter, but swarm away through the water, or else come to rest in a short time, in which case if the seat of their activity dries up they are blown away by currents of air, and so conveyed to other dead plants. Similar decompositions can be induced by moulds (*Eurotium*, *Mucor*, *Botrytis cinerea*, *Penicillium glaucum*) as well as by bacteria, and, in addition, the disintegration of wood occasioned by the mycelium of Dry-rot (*Merulius lacrymans*), the green-rot of trunks of oaks, and beeches, caused by *Peziza aeruginosa*, the mouldering of wood induced by the mycelium of *Polyporus*.

*sulfureus* and various other fungi, the red-rot, &c., all depend on similar disruptions of the organic compounds in dead plants, and result in the ultimate dispersal of these in the air in the form of carbon-dioxide, ammonia, nitric acid, and water.

Thus, ultimately, the exercise of this destructive activity only effects a return of the compounds just enumerated—the most important to plant-life—to the regions whence they had previously been withdrawn by the plants when living. Carbon and nitrogen, in particular, are set free from their bonds and given back to the atmosphere in the form and combination in which they are capable of being appropriated anew by living plants as food-material.

Considered from this point of view the phenomena of putrefaction and rotting appear as important and even necessary incidents in the history of the substances which are of the greatest importance to plants. Abhorrence of putrefaction is innate in us all, and everything connected with it—in particular, the entire race of bacteria—is looked upon with aversion. To estimate these processes according to their deserts requires a sort of self-abnegation. But when we overcome our repugnance and weigh the whole subject impartially, we come to the conclusion that the continued existence of vegetable life and of life in general depends upon the occurrence of putrefaction. If the untold numbers of plants which die in the course of a year did not rot sooner or later, but remained unchanged as lifeless forms, a certain quantity of carbon and nitrogen would be idle, being withdrawn from the sphere of activity and locked up, so to speak. Now, assuming this to be repeated year by year, a time must come when all the carbon and nitrogen would be imprisoned in dead plants. Thereupon, all life would cease, and the whole earth would be one great bed of corpses.

Not only putrefaction, but also the minute organisms which excite putrefaction appear in a more favourable light when viewed from this standpoint. Let such bacteria as act in the capacity of foes to the human race, ravaging town and village in the form of infectious diseases, be exterminated if possible; but annihilation of putrefactive bacteria would mean a disastrous interference with the cycle of life upon the earth. These latter are not to be reckoned as enemies but friends to human beings. The effect of their invasion of dead plants and animals is certainly first made manifest, not in the most agreeable manner, for some of the substances mentioned as being evolved in the early stages of the onslaught, viz.: various ammoniacal compounds, sulphuretted hydrogen, and the volatile fatty acids, are disgusting to us; but as decomposition advances these phenomena, which are so unpleasant to our senses, abate, and the action of putrefactive bacteria becomes ultimately a beneficent process of purification of the last remnants of dead organisms. The final result of the decomposition of organic bodies by bacteria has been termed mineralization. It is a fact that nothing is ultimately left behind, in the ground or water, of bodies decomposed by the indefatigable exertions of bacteria excepting some nitric acid and the small quantity of mineral food-salts which has been taken up by the living organism in its time and are now in the form of dust and ash.

By filling with water a glass which contains vegetable and animal remains in a state of putrefaction and swarming with bacteria, one is enabled to follow this process of mineralization from day to day. First, a decrease of the organic matter clouding the liquid, accompanied by simultaneous increase of ammonia and nitrous and nitric acids, is observed; then, after about two months, a complete clearing up of the liquid. The water is now colourless and odourless, but a precipitate has formed at the bottom, which contains, in addition to insoluble food-salts, bacteria in a state of temporary quiescence on the termination of their task and waiting till fresh prey becomes accessible. No doubt these processes occur in nature in just the same manner as in the glass of water, and the so-called self-purification of rivers, for example, has been rightly attributed to mineralization. It was long ago noticed that the water of such rivers as flow through great towns and consequently take up considerable quantities of animal and vegetable refuse contains no discoverable trace of all these impurities a few miles below the mouths of the drainage pipes and sewers. The water of the Elbe, which receives the refuse of the towns of Prague, Dresden, and Magdeburg, is so pure at Hamburg that it is there used for drinking purposes without protest<sup>1</sup>. The Seine, after taking up masses of rubbish in Paris, is already by the time it reaches Meulan, a distance of 70 kilometers, clear and pure again, and does not even exhibit there any traces of the organic matter received in the great city. Were it not for the activity of the putrefactive bacteria, this purification would never take place; and although the statement that putrefactive bacteria are the best of purifiers sounds at first like a paradox, it must be acknowledged to be consistent and based on experience.

## MECHANICAL CHANGES EFFECTED IN THE GROUND BY PLANTS.

All the alterations hitherto spoken of as being brought about in earth and under the influence of vegetation subsisting therein are reducible to chemical transpositions. Added to these, there are always certain purely mechanical changes. The penetration of the rhizoids of a rock-moss or the hyphæ of a crustaceous lichen into limestone is accompanied, as has been already stated, by a solution of part of the substratum and a mechanical separation of another part; the rhizoids or hyphæ, as the case may be, becoming imbedded amongst tiny detached fragments of the underlying stone. When the hyphæ and rhizoids die, the corresponding piece of the substratum is left porous, and admits air and water, whilst other plants are enabled to settle on it, although they may not perhaps possess the power of eating into stone and pulverizing it in the same degree as their predecessors. This is also true of the roots of Phanerogams. The food-seeking root-tips and their absorption-cells displace particles of earth as they insinuate themselves, and when they decay later on, the soil at those particular places is intersected by passages of varying size. No doubt these passages mostly collapse like the abandoned shafts and galleries of a mine, but some trace of root-action always remains behind in the shape of an

<sup>1</sup>This was written before the last outbreak of cholera.

increased looseness of the soil in the locality, a result of the greatest importance, inasmuch as it enables air and water to permeate to a depth much more easily and quickly by the ways that the roots have previously opened up. Dead roots rotting underground constitute, moreover, the source of the carbonic and nitric acids which help to render available the mineral constituents, and so serve the turn of subsequent generations of plant-settlers on the same spots, whilst they accomplish fresh disintegration of the substance of the soil.

If, however, the subterranean parts of plants are continually engaged in mining, and so change in various ways the position of the component particles of soil, the organs above ground exert an influence in some measure opposed thereto, in that they retain and bring to rest particles of earth which are set in motion by currents of air or water. In the section that treats of the absorption of nutrient salts by lithophytes, attention was directed to the fact that the dust pervading the atmosphere, and blown from place to place by the wind, is arrested to a remarkable extent by mosses and lichens. One need only detach a small tuft of the common *Barbula muralis*, which everywhere occurs on walls by roadsides, to convince oneself of the extent to which dust from the road is lodged amongst the leaves and stemlets, and of the tenacity of its adhesion. Moreover, not only such dust as rises from roads, but also that variety which, though not easily observed, yet fills the air of remote mountain-valleys, of arctic ice-fields, and of the most elevated parts of the earth's crust, is arrested in those localities by mosses and liverworts, and by many Phanerogams besides, the growth of which is similar to that of mosses. There is not much less dust clinging amongst the stemlets of the dark *Grimmias*, *Andreaeas*, and other rock-mosses, which grow in small cushion-like tufts on weather-beaten mountain crags, than is attached to the *Barbula* living by the dusty roadside. If one of the tufts in question is detached from its substratum, a fine powder composed of mica-scales, granules of quartz, chips of felspar, and a number of minute organic fragments pours out from between the moss-stems, whilst another portion of this finely powdered earth is left clinging to the leaves and stemlets, and is found to be regularly adnate to them.

It is never, however, the still fresh and living upper parts of these leafy moss-stems that arrest and carry dust, but always the older dead parts below. The lower dead half of the moss, whether still in a state of preservation or already rotting, is alone capable (in consequence of characteristic alterations in the lifeless cell-tissue) of holding fast the atmospheric dust. The under part of moderate-sized cushions of moss constitutes a compact mass composed half of imprisoned dust and half of brown lifeless moss-stems. These little cushions, clothing rocky crags, become a favourable site for the germination of a whole host of seeds, which are conveyed thither by the wind and detained in the same manner as the dust. The seedlings arising from these seeds send their rootlets into the subjacent portion of the bed of moss, where the interstices are full of dust or finely-divided earth. Here they find all the conditions prevailing necessary for their nourishment, and they expand, and, little by little, crowd out the mosses which received them so hospitably,

forming ultimately a bed of flowering plants, including in especial abundance representatives of the orders of grasses, pinks, and composites.

Many water-plants—in particular, aquatic mosses and algae—possess, in an almost greater degree than lithophytes or land plants, the power of laying hold of inorganic particles, and thus exercise a far-reaching influence as mud-collectors on the conformation of the ground. It is wonderful how plants are able to arrest large quantities of the fine sand hurried along by a flood, although they are exposed to the violent rush of the water. The tufts of the dark green alga *Lemanea fluviatilis* and of the aquatic moss *Cinclidotus riparius*, which cling to rocks in the cascades of clear and rapid mountain torrents, are so conglomerated by mud and sand that they cannot be freed therefrom until the tissue has become dry and shrivelled. *Limnobium molle*, which grows in the turbid waters from glaciers, has such an abundance of earthy particles adhering to it that only the green tips of the leaf-bearing stems are visible above the grey-coloured cushions imbedded in the mud. The felted masses of *Vaucheria clavata*, filling the channels of apparently clear, gently-flowing streams, are so mixed with mud that if a lump of this alga is fished out, the weight of mud clinging to it exceeds that of the alga itself a hundredfold. In these cases of submerged plants, it is, again, not the living but the dead parts which serve to arrest the mud. On lifting up a lump one sees clearly that only the uppermost and youngest prolongations of the filaments—those situated at the periphery of the algal cushion as a whole—are living and filled with chlorophyll; the fundamental mass has become colourless and lifeless. But these dead parts, which form a thick felt of interwoven filaments, alone retain in their meshes the finely-divided mud and sand in such surprising quantities; these particles slip off the green living parts without adhering to them. An important consideration in this connection is the fact that the dead cell-membranes swell up and become slightly mucilaginous, so that fine particles of mud lodge more easily in the soft swollen substratum thus formed. Wooden stakes stripped of bark and fixed in a strong current show this very clearly, as do also the trunks of trees that are thrown up by floods and lie stranded on the shore with their bared boughs projecting into the stream. However strong the current to which wood in that condition is exposed, it covers itself in a short time with a grey coat consisting of earthy particles brought down by the water. If a piece is cut off and exposed to the air, the earthy deposit does not become detached until the wood-cells have dried up and shrunk. As long as they are moist the particles of mud continue to adhere to them.

This mechanical retention and storage of dust by rock-plants and of mud by aquatic plants is of the greatest importance in determining the development of the earth's covering of vegetation. The first settlers on the bare ground are crustaceous lichens, minute mosses and algae. On the substratum prepared by them, larger lichens, mosses, and algae are able to gain a footing. The dead filaments, stems, and leaves pertaining to this second generation arrest dust in the air and mud in the water, and thus prepare a soft bed for the germs of a third generation, which on rocks consists of grasses, composites, pinks, and other small herbs, and in water

of pond-weeds, water-crowfoots, hornwort, and various plants of the kind. The second generation is produced in greater abundance than the first, and the third develops more luxuriantly than the second. The third may be followed by a fourth, fifth, and sixth. Each successive generation crushes out and supplants the one preceding it.

As on the rocky heights and in the roaring torrents of mountains, so also on the sandy plain and in the depths of the sea, a perpetual variation in the nature of the vegetation is taking place. At all times and in all places we see younger generations displacing the older and building upon the foundations laid by their predecessors. The first settlers have a hard fight with uncompromising elements to seize possession of the lifeless ground. Years go by before a second generation is enabled to develop in greater luxuriance upon the earth prepared by the first occupiers; but there is no cessation in the productive and regulative effects of vegetable life, and its energy and aptitude in the work result in the erection of its green edifices over wider and wider areas. New germs are established upon the mouldered dust of dead races, and others on the plant forms adapted to the altered substratum, and so, for hundreds and thousands of years, the changes go on, until at length the tops of forest-trees wave above a black and deep soil, the battle-field of a number of bygone generations. Thus, the life of plants, like that of the human race, has its epochs and its history: as in the one so in the other a continual struggle prevails; processes of ousting and of renovation are always in progress, and there are ever new arrivals upon and departures from the scene.

## CONDUCTION OF FOOD.

---

### 1. MECHANICS OF THE MOVEMENT OF THE RAW FOOD-SAP.

Capillarity and root-pressure.—Transpiration.

#### CAPILLARITY AND ROOT-PRESSURE.

Unicellular plants make use individually of the food material which they absorb from their surroundings, and work it up into the organic substances which they require for their structure and increase in bulk, and also for the production of future generations. In all plants composed, on the other hand, of aggregates of cells, there is a division of labour. Of the protoplasts occupying the cell-cavities of such larger plant-structures, one part provides for the absorption of the water and food-salts, another for the taking in of the gases which are used as food, and yet another part works up this food into organic substances for constructive purposes. The centres in which these various industries are carried on are frequently situated at some distance from one another, and it is obvious that there must not only be some communication between the various regions of activity, but that active forces must come into play which will effect the transport of the food from the cells whose function it is to receive it, to those in which it is to be elaborated into building material. It is evident that the greater the distance is between the various centres of the plant in question, the more difficult will be the performance of this task. In aquatic plants and lithophytes, all of whose superficial cells have the power of taking in nourishment from their environment, these distances are proportionately small, while they attain their greatest dimensions in land-plants whose roots are embedded in the earth, and whose leaves are surrounded by air. In trees the food materials which are taken up by the absorbing roots beneath the ground must frequently travel far more than 100 metres before reaching the topmost leaves. The path to the summit is very steep, and the fluid in rising must be able to overcome the force of gravitation, which has no inconsiderable significance at heights such as these.

Naturally, desire for knowledge has at all times directed attention to this phenomenon, and the most diverse attempts have been made to explain by what means the food-sap taken in by the roots of trees is enabled to reach their summits. It was first considered to be in virtue of *capillarity*; that just as oil, alcohol, or water, is drawn up the wick of a lamp, the liquid food can rise in the delicate tubular cell-formations called vessels, which, united together in groups or

bundles, traverse the stems and leaves of plants. But the vessels are closed in above and below, and therefore it is impossible that capillarity should be sufficiently developed in them. At best it could only raise the sap a trifling distance, and could never convey fluid to a height of many metres. It is a striking fact that in many plants the ascent of the sap is most vigorous after the evaporation from the superficial parts exposed to the air has been weakest. The so-called "weeping" of vines, *i.e.* the outflow of sap from the flat surface of a cut vine-branch, does not take place in summer and autumn, immediately after the branch has been fully adorned with foliage, and when its extensive leaf-surfaces have given up large quantities of moisture to the surrounding air; it occurs at the end of the winter sleep of the plants, when the brown branches rising above the ground are still in a bare and leafless condition. The cause of the ascent, or at least of the ascent in the lower leafless branches, must therefore be sought for in the absorbent roots, and it may be assumed that here the same causes are at work which induce the fluid food materials of the surrounding earth to enter the superficial cells at the root-tips.

It has already been shown that the contents of these cells suck up the water of the nutritive ground with great force in consequence of the chemical affinity they have for it, or in other words, that the fluid reaches the interior of plant-cells by *endosmosis*; it has also been mentioned that in consequence of the taking in of water the volume of the cell-contents increases, producing pressure from within outwards on the cell-wall, and the cell swells and becomes turgid. From this one of three cases might be deduced:—first, suppose that the cell-wall is so composed throughout that it allows the entrance of water into the cell, but not its exit, and that consequently the cell-contents absorb water, but that a filtration of the same towards the exterior cannot take place. Granted this hypothesis, the cell-wall by virtue of its elasticity would yield to the pressure of the cell-contents, but only within the limits of that elasticity; hence a condition of tension would be produced, in which the reciprocal pressures of the cell-wall and cell-contents would be in equilibrium. In the second case, suppose that the pressure of the cell-contents is greater than the force of cohesion between the molecules of the cell-wall, this consequently ruptures, and the cell-contents issue from the rent which is formed. This phenomenon is seen in certain pollen grains when placed in water. In half a second the cells absorb so much water that they double their volume; the cell-contents still absorb the fluid, and the cell-wall can at length no longer withstand the pressure; it bursts, and the contents, from which the pressure is now removed, pour through the opening, and are diffused in the surrounding water.

There is a third case possible. Suppose that in a given cell the opposite walls are not of identical structure; that the wall which is in contact with the damp earth is so organized as to allow the entrance of water, but not its filtration to the exterior, while the opposite wall offers only a slight resistance to such filtration; then by the increasing pressure of the cell-contents fluid will be forced through that wall which offers least resistance, and the greater the affinity of the cell-

contents for the fluids in the nutritive earth, the more abundantly and energetically will this be carried on. The phenomenon can be well seen in some moulds, especially *Mucor Mucedo*, which makes its appearance in such quantity on succulent fruits; and in the mycelium of the so-called Dry-rot, *Merulius lacrymans*. Fluids are sucked up by the lower portions of the tubular cells which cover the nutritive substratum, and expelled again through the walls of upper parts of the same cells, which project freely into the air. These upper portions of the mycelium cells appear as though ornamented with tiny dewdrops, which in the case of the Dry-rot coalesce and attain to a considerable size. Damp woodwork in cellars, where this fungus has established itself, is often thickly besprinkled with the drops which have been excreted on the surface, and if a lamp is brought into the darkness, and the infected places illuminated, hundreds of these tiny drops sparkle and glitter like the "jewels" in a cave of stalactites. Suppose then that such a cell, one wall of which allows fluid to enter, is attached by the wall opposite to that through which the fluid enters, to another cell; then this second cell will absorb the liquid, and, if tubular, the sap may rise higher and higher in it, and by the pressure of the liquid continually arising from below, even be forced through other higher cells which are capable of filtration. Naturally the rising current of sap thus generated follows the line of the least resistance; if then the cell-tissue where this action terminates is perforated by canals ending in pores on the surface, the fluid will emerge from these pores in the form of drops. This actually happens not only in many large-leaved Aroids, but also in plants growing in the open country if the air which passes over the leafy parts above the ground be very humid, and the soil in which the roots are buried proportionately warm. In many plants with succulent foliage, drops of water may be seen issuing from the thin-walled cells and pores of the leaves when the almost saturated air becomes cooled after sunset, while the soil, round about the absorbent roots, having been exposed all the day to the sun's rays, retains its higher temperature. Young blades of corn have rows of such drops, which look exactly like dewdrops, and have often been mistaken for them. This extrusion of water from the leaves can easily be produced artificially by placing the plants in a saturated atmosphere, and at the same time slightly warming the earth round the roots. There is no doubt that the sap which exudes from the leaf-pores originates in the nutritive soil, and is taken up by the absorbent cells of the root; from these the vessels and cells of the main root and stem, through which the sap can filter, carry it up to the leaves. If, therefore, we cut across a stem a little distance above the ground, we shall see the sap, which has already accomplished half its journey, welling up as drops on the cut surface; *i.e.* we shall see the remarkable phenomenon called "weeping", of which mention has already been made. The quantity of sap which flows from such a cut surface is in many cases astoundingly great. In Java certain *Cissus* plants, belonging to the family of lianes and living in damp woods, are actually made use of as vegetable springs. The watery sap flows so abundantly from a cut branch that in a very short time it will fill a glass, and forms a cool and

refreshing beverage. Many Araliaceæ also furnish a sap fit for drinking. Some native Indian genera which are used as vegetable wells have on this account received the name of "plant springs" (*Phytocrene*, e.g. *P. gigantea* and *bracteata*). If the young flower-stalk of *Agave americana*, an American plant which is cultivated in European gardens under the name of the "hundred years' aloe", be cut across, in twenty-four hours about 365 grammes, and in a week more than 2500 grammes of sap will flow out. This exudation continues for four to five months, and a vigorous *Agave* will produce in this time as much as 50 kilogrammes of sap, which will ferment, since it contains both sugar and albuminous substances, and is indeed used by the Americans in the preparation of an intoxicating drink called "pulque". The quantity of sap which exudes from vines is also very great. A branch  $2\frac{1}{2}$  cm. thick, cut across  $1\frac{1}{2}$  m. above the ground, produced within a week over 5 kil. of sap. In a week, from the cut stem of a rose, more than 1 kil. was exuded. From maples and birches a proportionately large amount of sap can be obtained, when the trunks are cut about a metre above the ground. The sap which flows from species of maple contains pure crystallizable sugar, and in some North American species this is present in such abundance that it was found to be worth while to collect the sap, at least in former times.

It should be noticed that the volume of the exuded sap is in all these cases greater than the volume of the root together with that of the stump of the stem from which the sap is forced out, and this is a proof that it does not consist only of the water which was contained in the root and stem stump at the time of cutting, but that there is a continual upward current of sap, and that the absorbent cells of the roots, for a long time after the operation, continue to draw up water from their environment.

An ingenious experiment was performed at the beginning of last century in order to ascertain the amount of pressure by means of which the sap is forced from the cut surface of the vine and other stems. A vine stem without branches and about the thickness of one's finger was cut across in the spring at a height of about 80 cms. above the ground, and on the root-stock was fixed a glass tube with a double bend, in such a way that one end fitted exactly over the cut surface of the stump, and the tube was then filled with mercury. By the pressure of the sap which welled from the cut surface the mercury was forced up the tube, and in a few days it actually reached a height of 856 mm. The weight of a column of mercury 760 mm. high is equal to that of a column of air as high as the atmosphere of the earth, or of a column of water about 10·3 m. high, and consequently the pressure by which the sap is forced out of the vine is considerably greater than the weight of one atmosphere, or of a column of water of the height mentioned. From these data it has been estimated that the sap can be raised through 11·6 m. by the pressure originating in the absorbent cells of the root. The pressure is naturally greatest in the lower portions of a stem, and gradually diminishes towards the higher regions; the ascending current of sap to which it gives rise is also not uniform, but shows daily, and even hourly, fluctuations. Moreover, the quantity of

sap exuded, neglecting these said fluctuations, is greatest soon after the stem is cut, and then becomes gradually less until finally the outflow ceases entirely with the death of the stump.

The magnitude of the pressure, and the quantity of the sap forced up by the absorptive power of the cells, vary with the circumstances of the plants considered. The pressure appears to be greatest in species of vine, and in the vine stem, as already remarked, it will support the weight of a column of mercury 856 mm. high. In the stem of the Foxglove it equals the pressure of a column of mercury 461 mm. high; in the stem of the nettle the column is 354 mm.; in the poppy stem 212 mm.; in the stem of a bean 159 mm.; and in the trunk of the White Mulberry tree 12 mm. high. In the majority of herbaceous plants this pressure is quite sufficient to drive the sap from the root-tips up to the leaves and top of the stem; but this is not the case with leafy trees and pines, with palms and creeping and climbing plants. Although watery fluid can be raised according to the above calculation to a height of 11·6 m. by root-pressure, there is still a great distance between this level and the leaves of such trees and climbing plants, which may be as much as 160 m. high; and the question which presents itself is this: By what means is the sap carried to the higher regions from this level to which it is raised by root-pressure?

It may be supposed that cells are present at the various heights in the stem to which the water is driven, which act in a manner similar to those of the root; i.e. cells which actively absorb, whose cell-wall on one side only slightly resists filtration, and which therefore are able to force up the sap a little higher. The results of the following experiments seem to support such a supposition. If a piece of a branch be cut from the middle portion of a tree, and the lower end be peeled and placed in water, sap will flow out from the upper cut surface with considerable force. The same thing occurs when a leafy branch is placed in water so that its leaves are submerged, while the upper cut piece of the branch projects a good way out of the water. In this case the cells of the leaves must function as the absorptive cells. However, even if, as is probable, parenchymatous cells are to be found at all levels of the plant stem behaving exactly like the absorptive cells of the root, this arrangement would scarcely suffice in all cases to carry the sap to its destination. Atmospheric pressure as well as the rarefaction of the air observed in the vessels of the stem during the summer have been made use of in explaining the upward current of the sap, and this rôle may actually belong to these factors; but all these mechanical powers are quite overshadowed by that one which has been termed by botanists "*Transpiration*".

## TRANSPIRATION.

By transpiration of plants we mean the act of giving off aqueous vapour to the surrounding air—briefly and in plain terms, the perspiring of plants. Vapour escapes from the cells of the plant which are in contact with the air, the formation of these cells being specially adapted to the process of evaporation, just as it is given

off from moist inorganic bodies and exposed liquids. Of the materials which are held in solution in the sap of plants, only those which have the property of passing from the fluid to the gaseous condition, at the same temperature which transforms water into water-vapour, can evaporate with this fluid. All the others remain behind, and the natural consequence is that the sap in the transpiring cells becomes more concentrated. If water, which contains in solution extremely small quantities of sugar, organic acids, nitric, sulphuric and phosphoric acids, and salts of potassium, calcium, and iron, be set to evaporate slowly in a shallow dish, it will gradually come about that only a thin layer of fluid is left on the bottom of the dish; but this now is seen to consist of a very concentrated solution of the substances mentioned; i.e. of the sugar, organic acids, and the various salts. It has also all the properties of such a concentrated solution, i.e. it has the power of sucking in water in the liquid condition from its surroundings. In the same way the contents of a cell in contact with the air become more concentrated by evaporation, and thus obtain the power of abstracting water from the environment of the cell, that is to say, of sucking it up. If two adjacent cells contain sap of the same density, whilst only one of them has the power of exhaling water, the condition of equilibrium between them will be destroyed. However, the balance naturally tends to be restored, and the cell whose sap has become more concentrated by the evaporation of water, takes up watery fluid from the neighbouring cell. Now picture a chain of cells containing abundance of sap connected with one another by cell-walls through which fluid can filter, and let them be so arranged that only the uppermost member of the chain is in contact with the atmospheric air. The sap of this uppermost cell having become concentrated by evaporation will first of all exert a suction on the cell immediately below. As fluid is withdrawn from this second cell, its sap also undergoes concentration, and in consequence produces suction on the third cell, the third in like manner on the fourth, the fourth on the fifth, &c., passing from above downwards. In this way innumerable compensating currents are set up between the adjoining cells, which, however, never lead to true equilibrium as long as evaporation continues in the cell in contact with the air, but combine together to form a single ascending stream.

Such a current actually exists in all living plants which evaporate from the portions above the ground and in contact with the air, while their lower extremities are embedded in a damp nutritious soil. This has been termed the *Transpiration Current*. Its source is the fluid which has been drawn from the earth by the absorptive cells and brought within the sphere of the living cells of the plant; we may retain for this fluid the old and very appropriate name "crude" or "raw sap". Its direction and destination are determined by the position of the evaporating cells, and its path is through the wood, which in tree-trunks is inserted as a huge layer between the bark and the pith; in lesser stems it passes through the bundles and strands of woody cells and vessels which traverse them, being connected, deep under the ground, by groups of parenchymatous cells, with the absorptive cells of the young rootlets, or with the hyphae of the mycelial mantle, which replace the



Fig. 60.—Olive Grove on the Shores of Lake Garda.

absorptive cells (beech, &c.). These bundles pass above into the leaves, forming there the "veins" of the leaf-blade, which spread out into an extremely fine network of tiny strands, and terminate quite close to the evaporating cells on the surface. That the wood actually forms the conducting tissue of the transpiration current is satisfactorily demonstrated by the existence of old trees whose trunks have long been hollow, whose pith is disintegrated and fallen away, and which have also been deprived of bark around their base. In the olive plantations at Lake Garda, one of which is reproduced in figure 60, many trees are to be seen in which the lower part of the trunk is not only hollow and without bark, but is also often tunnelled and split, so that the upper part of the tree looks as if it were raised on stilts. The only communication between the soil and the upper part of the tree is by means of these props, which are continuous with the roots below and are composed entirely of woody cells and vessels. And yet these olive-trees are still vigorous, putting out new branches and leaves every year, and blossoming and producing fruit; and they derive their necessary food from the ground by supplies which have no other upward path than the wood of these props.

Moreover, by repeated experiments it has been proved that the bundles of woody cells and vessels which are united together into a woody cylinder, inserted between the pith and the cortex in the trunks and stems of trees and shrubs, serve as conductors of the transpiration current. If a ring of cortex is removed from the stem of a leafy plant, whose leaves are transpiring in dry air, and are supplied with water from below by the transpiration current, this flow of sap to the leaves will not be interrupted, and the leaves remain firm and tense. But as soon as a piece of the wood is removed or the above-mentioned strands are cut through, even though the cortex be left entire, the flow to the leaves stops immediately, and they become flaccid and hang down in a withered condition.

The cellular formations of the wood and strands, which function as the conductors of the crude nutritive sap to the leaves, are—as already mentioned—*wood-cells* and *wood-vessels*. Formerly the idea was held that these structures served for the passage of air, and it was believed that they were analogous to the respiratory organs—the so-called tracheæ—of insects; therefore these wood-vessels were also called "tracheæ", and the wood-cells "tracheides". The wood-cells are elongated chambers, on an average 1 mm. long and 0·05–0·1 mm. broad, and their walls are unequally thickened, either by reticulate or annular bands, or spiral threads projecting slightly from the inner wall into the lumen, or by so-called bordered pits, which are represented in fig. 10<sup>1</sup> and fig. 10<sup>2</sup>. The wood-vessels are tubular, and very long in proportion to their width, which is never more than a fraction of a millimetre; they extend uninterruptedly through stalks, branches, leaves, perhaps even through the entire plant from the root-tip to the crown. They are composed of rows of cells whose separation walls have been broken down. The walls of the wood-vessels exhibit similar thickenings to those of the wood-cells or tracheides. When the chambers and tubes of the wood, with their bordered pits and projecting bands, are fully developed, the living protoplasm which carried on the building forsakes the

scenes of its activity, and consequently in fully formed wood-cells and vessels living protoplasmic contents are wanting. They must be regarded in a certain sense as dead structures, for they have no further power of growth, and the reciprocal pressure of wall and contents observable in absorptive cells and other cell-cavities occupied by living protoplasm, which has been termed "*turgescence*", is never seen in them.

In the walls of the wood-cells as well as of the vessels, woody material (Lignin) is deposited. It appears to be in consequence of this that they are much less capable of swelling than are cell-walls which consist chiefly of cellulose. The amount of sap which presses its way in between the groups of molecules of the lignified walls, and with which these walls are saturated, is also comparatively very small. On the other hand, of course, this imbibed sap is conducted much more quickly through the lignified walls of the cell chambers and tubes than through non-lignified walls. More fluid is carried up by the intermolecular stream through the woody walls of the cells and vessels than by the ascension of the raw nutritive sap in the interior of the wood-cells and tubes. If no evaporation is going on from the leaves, or if this is only very slight, the vessels and cells become filled with sap. As soon as transpiration becomes active, part of the sap is taken up, and if fresh supplies do not arrive quickly enough a limited amount of air can get in temporarily, which of course must be in a very rarefied condition on account of the obstacles which oppose its entrance. The passage of the sap is quicker through the non-septate vessels than through the much shorter woody cells. The sap on its way through the latter, to the transpiring leaves, must filter through innumerable transverse walls. This filtration will of course be materially helped by the bordered pits with which the wood-cells are so regularly provided; for the extremely delicate membrane which is stretched between the two cavities of such an apparatus at any rate allows the sap to pass through very easily. The bordered pits are exactly like clack-valves, and they also appear to regulate the sap-stream, though the way in which they do this is not yet completely understood. The nearer the path of the raw sap approaches to the spots in which evaporation is being carried on, the greater is the number of cells in the sap-conducting strands, while the vessels in the same become fewer and fewer. The termination of the whole sap-conducting apparatus consists entirely of cells whose walls are stiffened by spiral bands on the inside. Between this termination and the transpiring cells some parenchymatous cells with living protoplasmic cell-contents are interposed, whereas, it must again be insisted, the tubes and chambers composing the sap-conducting apparatus have no living protoplasm in their interior.

The whole mechanism for the transmission of the raw nutritive sap may be considered as a system of tubes and chambers provided with clack-valves, into which the fluid taken up by the absorbent root-cells is forced, and through which it is conducted to the transpiring cells of the green leaves or of the green cortex, which takes the place of the green leaves in leafless branches. This does not exclude the activity of cells at certain levels, as it were at intermediate stages of the road traversed by

the current, which have the power of invigorating the stream, of hastening it if necessary, and also of lessening it under certain circumstances. Also it is arranged that in case of need fluid nourishment in the higher regions of the stem may reach the leaves by side paths.

The cells which by means of the exhalation of aqueous vapour into the atmosphere originates the transpiration-current are, as already mentioned, not far from the terminations of the sap-conducting apparatus. In some mosses they are freely exposed to the air. In the Polytrichaceæ and several other mosses (*Barbula aloides*, *ambigua*, *rigida*) they form short chains of cells like strings of pearls, or bands projecting from the grooved concave upper surface of the tiny leaves (see fig. 61<sup>2</sup>). Again, among the liverworts are forms, e.g. *Marchantia polymorpha*, which contain large characteristic air-chambers in the body of their green leaf-like thallus (fig. 61<sup>1</sup>). On the floor of this chamber are green cells which are so grouped together

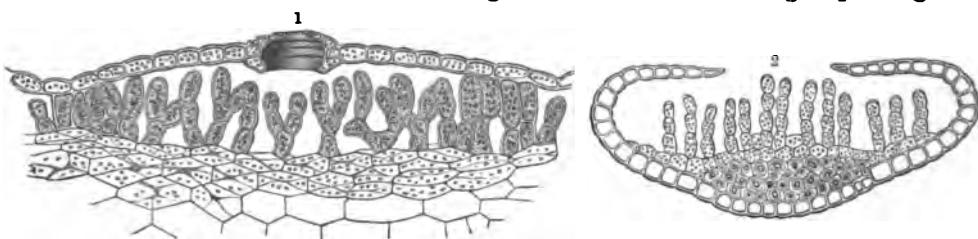


Fig. 61.—Transpiring Cells.

<sup>1</sup> Vertical section through an air-chamber of the Liverwort *Marchantia polymorpha*;  $\times 300$ . <sup>2</sup> Vertical section through a leaf of the Moss *Barbula aloides*;  $\times 350$ .

as to remind one of the shape of the Prickly Pear (*Opuntia*). These green cells are thin-walled, and it is from them that water is evaporated. They are not quite freely exposed, like those of the mosses mentioned above, since the roof of the chamber, composed of transparent cells, is extended over them; a chimney-shaped passage, however, is left open through the roof of each chamber by which the water-vapour given off from the opuntia-like cells can escape. These *Marchantias* furnish a transitional form between the freely exposed transpiring cells on the upper surface of the leaf of the moss and those of flowering plants. In flowering plants the transpiring cells are situated as a rule in the interior of the green leaves, and also in the green cortex of leafless branches, forming a part of that green tissue which has been termed *chlorenchyma*, or when in the leaves, *mesophyll*.

Leaves may be described as consisting of cells filled with leaf-green, or chlorophyll, placed closely together and joined into layers above one another so as to form a soft mass of tissue containing abundance of sap; this green tissue pierced by the branched water-conducting strands whose ultimate divisions terminate in the tissue mass; the whole surrounded and shut in by a firm cuticle which is perforated in many places by stomata. Cellular passages are also regularly arranged for the purpose of conducting away the organic materials manufactured in the green cells, whilst groups of cells for the support of the whole, serving as beams, strengthening props, and the like, are placed at definite points.

In most thin membranous leaves the upper and under sides are differently constructed, and the difference is not confined only to the cuticle, but is also plainly recognizable in the green tissue. The green cells below the epidermis on the upper side of the leaf have the form of prisms, cylinders, or short tubes, and are arranged very regularly in ranks and files. In the leaves of plants belonging to the lily tribe, they lie with their long axes parallel to the surface; but in most other plants these cylindrical cells have their smaller side directed to the surface, and stand side by side like palisades, with only very narrow air-passages between them. Below these palisade-cells, and bordering on the epidermis of the under side of the leaf, is another stratum of cells of a much looser texture (see fig. 62<sup>1</sup>). The cells of this under layer are not so crammed with chlorophyll, and therefore appear a lighter

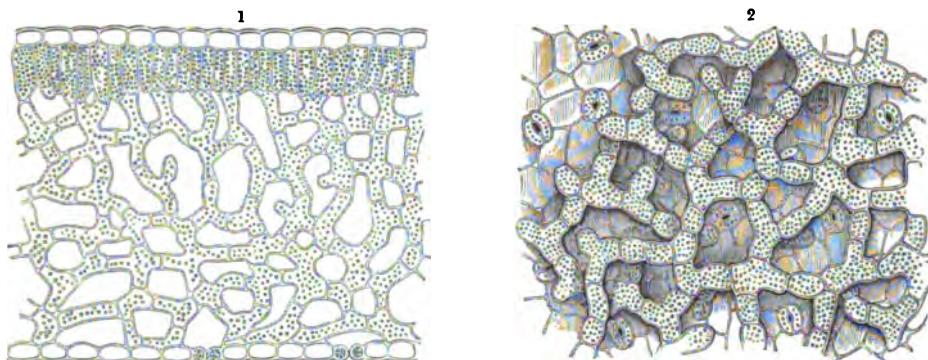


Fig. 62.—Spongy Tissue.

<sup>1</sup> Vertical section through leaf of *Franciscea eximia*. <sup>2</sup> Spongy tissue in leaf of *Daphne Laureola*.—The epidermis and palisade cells of the upper side of the leaf are removed. The epidermis of the under side of the leaf, with its stomata, can be seen through the spaces in the spongy tissue;  $\times 320$ .

green than the palisade-cells. In shape they are elliptical, rounded, angular, sinuous, or generally very irregular; usually they possess protuberances which project in various directions, and they are so arranged that the outgrowths of adjoining cells come into contact with one another. It looks as if the neighbouring cells were stretching out their arms and extending their hands to one another, and consequently these cells have been called "many-armed cells". When several adjoining stellate cells are connected together in the manner just described so as to form a tissue, lacunæ and passages are seen in the tissue, which are broken through by the joined arms of neighbouring cells as if by pillars, couplings, and bridges. The whole tissue has the loose perforated appearance of a bath sponge, and is called accordingly *spongy tissue*, or *spongy parenchyma* (see fig. 62<sup>2</sup>).

This spongy tissue is the proper place for transpiration. Nowhere else in the plant are the conditions governing this process so well fulfilled as just here. The surfaces of the cells are rendered large in proportion to their size by their out-growths; and they impinge as far as possible on the larger or smaller lacunæ, gaps, and passages filled with air, which all communicate with one another, thus constituting an unmistakable ventilating system.

Since the spongy parenchyma in the leaves described does not lie freely exposed,

but is shut off from the atmosphere by a firm cuticle through which water-vapour can only penetrate with great difficulty, the aqueous vapour which is exhaled by the branched and other cells of this parenchyma would saturate the lacunæ, and further evaporation would be thereby prevented. There must, therefore, be a direct communication with the outer air surrounding the leaf; the epidermis of the leaf must possess apertures through which the water-vapour can escape. The already repeatedly mentioned *stomata* are to be looked upon as such apertures.

Stomata arise in this way; in a particular epidermal cell a partition wall first of all divides it into two cells. This cell-wall splits, and the cleft widens, forming a short canal which pierces the epidermis, and constitutes a connection between the outer air and the air-containing lacunæ in the interior of the leaf. This short canal is called the *pore* of the stoma, and the two cells which border it are termed *guard cells*. These two cells regulate the outrush of aqueous vapour, *i.e.* of that vapour which has been excreted by the thin-walled cells of the spongy parenchyma, and passed into the adjoining passages in the interior of the leaf. That cavity which is placed immediately beneath the narrow, short canal of the stoma, and is connected by passages with other spaces further within the green tissue of the leaf, is termed the *respiratory cavity*.

The number of the stomata or transpiration-pores which pierce the epidermis of the leaf varies very considerably. In the leaves of cabbages (*Brassica oleracea*) in 1 sq. mm. of the upper surface there are nearly 400, and on the under side over 700. In the leaves of the olive-tree, on the same extent of surface of the under side, over 600. Succulent plants have remarkably few stomata. On 1 sq. mm. of the leaves of the House-leek (*Sempervivum tectorum*) and of the yellow Stone-crop (*Sedum acre*) only 10–20 are to be met with. In the majority of cases, on a similar extent of surface, between 200 and 300 stomata are to be found. The under side of an oak leaf, 50 sq. cms. in area, showed over two million stomata. They are in most cases scattered fairly uniformly over the surface of the leaf; on the leaves of grasses and pines, as well as on the green stalks of the horsetails, they form straight regular rows which run longitudinally; on the leaves of some species of saxifrage (*Saxifraga sarmentosa*, *japonica*, &c.) they appear crowded together in small isolated groups; and on the leaves of the *Begonia* they are generally to be seen side by side in pairs. Obviously they are principally developed just where the epidermis overlies spongy parenchyma, and as in the majority of cases this parenchyma is situated towards the under side of the leaf, the greater number of stomata are to be found on this side.

In most flat membranous leaves, which have one side directed towards the sky and one towards the earth, stomata are entirely wanting on the upper surface, being restricted to the under side. An exception to this is afforded by the orbicular flat leaves which float on the surface of water, *e.g.* those of the floating Pond-weed (*Potamogeton natans*), of the Frogbit (*Hydrocharis morsus-ranae*), and of the water-lilies (*Nymphaea*, *Nuphar*, *Victoria*). These are covered with stomata on the upper side, while on the lower side, which is in contact with the water, stomata are

entirely absent. On the upright leaves of flags, asphodels, amaryllis, and various other bulbous plants, and on the vertical leaf-like structures (phyllodes) of the Australian acacias, as well as on some of the needle-like leaves of conifers, the stomata occur on both sides in almost equal number. In the mimosas and various other plants, having, in common with the mimosas, the characteristic faculty of altering the position of their leaflets when stimulated externally, numerous stomata are found on both sides of the leaf.

Most stomata are elliptical when open; rarely circular or linear. The length of stomates varies between 0'02 and 0'08 mm., the breadth between 0'01 and 0'08 mm. Pines, orchids, lilies, and grasses have the largest stomata; water-lilies, olives, and some fig-trees, the smallest.

The stomata in the epidermis, the passages and cavities below them into which the thin-walled cells of the green tissue evaporate water, and the strands through which the sap is conducted from the roots to the green tissue, all work in connection with one another like the various parts of a machine. Each portion of the mechanism helps and depends upon the others, the immediate result of the common work being always the elevation of that nutritive fluid which is brought by the absorptive roots into the plant. In the main, therefore, the result obtained by transpiration is the same as that which root-pressure aims at, and it might be thought (taking for granted the truth of the above statement) that either root-pressure or transpiration is superfluous. Or perhaps transpiration and root-pressure work in a complementary manner together. Perhaps the conditions between the two forces are so arranged that the fluid taken in by the absorptive cells from the nutritive soil is forced up to a certain level by root-pressure, and from thence is promoted to still higher levels by means of transpiration? This would suggest a comparison with the raising of water from a spring situated in a valley-basin surrounded and shut in by mountains. In the depth of the basin exists underground water which is fed by the subterranean supply coming from the mountains. According to the pressure of this supply, the water in the lower earth-strata of the basin rises to a certain height. This pressure is not strong enough, however, to drive the water to the surface of the basin, and in order that it may reach this, it is necessary to employ a pump, which will reach down to that stratum of earth which is saturated by the underground water. But the level of this water differs in summer and winter. It depends also upon the amount of rainfall on the neighbouring mountains, which may undergo great fluctuations. In some years the underground water in the spring has almost risen to the upper opening; at other times only the deepest strata of the valley-basin contain water. The pump, by which the water has to be raised, must be constructed with all these possibilities in view, and must be so regulated that the absorbent action is felt as far down as the deepest position which the underground water is known to take.

Transpiration behaves in like manner in the portions of a plant above ground, and its action on the fluid food taken in by the roots may be compared with that of a suction-pump. It would be a quite inadequate arrangement if the sucking action

produced by transpiration could only reach down to the highest level attained by the water which has been forced up by root-pressure, and precautions must be taken that, in case of the abatement of the root-pressure, water would be raised from the lower positions up to the transpiring cells, and that under certain conditions the action of transpiration should reach even to the absorbent cells at the root-tips. It has been shown by experiments that plants with large leaves lose in the summer more water by transpiration than is forced up into the stem by root-pressure, and yet the leaves do not become faded. The conclusion drawn from this is that at certain times the effect of transpiration makes itself felt down from the leaves through the stem as far as the root-tips. It has also been shown that in many plants, just when the most active evaporation is taking place in the leaves, none, or only very little sap is forced into the stem by root-pressure. If the stem of a vine be cut across in the height of summer, when the green leaves have been unfolded some time and are transpiring actively, no "tears" are seen on the cut surface of the stump, no drops are pressed out. The vessels contain rarefied air but no sap, and water can be sucked through the stump by the vessels even in the direction of the root.

Let us pause here in order to get a clear idea of the relations between transpiration and root-pressure. Given the conditions for an abundant evaporation from the aerial portions of a plant—*i.e.* a fairly dry air, water, and an appropriate development of transpiring surface—then the action of root-pressure is diminished, while that of transpiration is increased, and governs the whole of the movement of the sap. If, on the other hand, the conditions for evaporation from the aerial portions of the plant are unfavourable—if the air is very damp, or if the branches of the plant are not yet in leaf—then root-pressure comes into play, and, supported by cells with absorbent contents which occur in the higher regions of the plant, can force up the sap to the tops of trees and to the highest shoots of vine-branches which remain leafless all the winter. So far, therefore, root-pressure can supersede and replace transpiration, a fact of great importance in places where the air is sometimes very damp, and in countries where the trees and lianes shed their leaves in autumn; at the commencement of the next period of vegetation they have not yet put out their new foliage, and therefore do not possess a sufficiently large transpiring surface. It is very probable that in the autumn, when preparing for the winter, certain cells in trees and lianes provide themselves with materials by means of which in the coming spring they may exercise a very strong sucking action. This would also partly explain how it comes about that in the spring there is such a strong upward current of sap in the still leafless trees and vine branches, and that the water is conducted up even to the topmost shoots of lianes 100 metres long, which have shed all their leaves in the previous autumn.

A perfect substitute for transpiration in the form of the pressure produced by the absorbent cells is seen in moulds, in the already-mentioned dry-rot fungus, and generally in leafless cryptogams: possibly also in those orchids possessing neither green leaves nor stomata, and in other humus plants (*saprophytes*) such as the

*Monotropa*, mentioned earlier on, which stands in such a peculiar relation to the mycelium of fungi. On the other hand, in most green flowering plants which bear leaves, a complete replacement of transpiration, continuing for a long time, is not an advantage. Experience has shown that green leafy plants, when kept for a long while in an atmosphere saturated with vapour, cease to grow and become unhealthy; they lose their leaves, and at length succumb altogether. This happens even if the amount of light, the temperature of the atmosphere and of the earth, the composition and humidity of the soil, in short, if all the other conditions of life are the most favourable that can be imagined for the plants in question. It follows from this that it is not immaterial to leafy plants how the sap reaches the leaves, whether it is drawn up by transpiration, or forced up by root-pressure. If the leaf transpires, water, in the form of vapour only, is given off to the atmosphere; all the materials which have been brought in solution from below to the leaves remain behind in the cells of the leaf. If, on the other hand, fluid water is pressed from the pores of the leaves by root-pressure, salts, sugar, and other compounds are always to be found in the exuded drops, having passed through the cell-wall in solution in the water. When it is a question of secreting sugar as a means of alluring insects, or salts for a protective covering, such an exudation cannot advantageously be given up, but is on the contrary a fundamental part of the economy of the whole plant. If this is not the case, and if materials which have a part to perform in the leaf by the formation of organic substances are exuded with the drops of water, and the drops falling from the surface of the plant trickle to the ground, there is loss of material, which does not contribute to the advantage, but rather to the detriment, of the organism.

The signification of transpiration may be explained in this way. By transpiration not only is water brought from below to the more highly situated parts of the plant, but nutritive salts in solution are also conducted to the green tissue of those branches and leaves which are exposed to light and air. The greater part of the ascended water is only used as a medium for the transmission of mineral salts, which have been taken from the soil into the plant. When it has reached the leaves, most of the water evaporates into the atmosphere, while the salts conducted by it into the green tissue remain behind, in order to take part in the chemical changes by which organic compounds are manufactured out of the raw materials. These salts are indispensable here, and transpiration is therefore also necessary in a corresponding degree. Without transpiration, it would be impossible that plants, whose green branches and leaves are surrounded by air, or that trees, which rank before all other plants on account of their superior size, could be properly nourished; consequently transpiration must be regarded as one of the most important life-processes of terrestrial plants.

---

## 2. REGULATION OF TRANSPERSION.

Means of accelerating transpiration.—Maintenance of a free passage for aqueous vapour.

### MEANS OF ACCELERATING TRANSPERSION.

Aquatic plants do not transpire; therefore they do not require either vascular bundles or stomata. Neither trees nor shrubs grow under water, and even the largest Florideæ and the most gigantic sea-wracks have no wood nor stomata. These structures are on the other hand very important for land plants, and in these they are developed in extraordinary variety. When one considers how much the humidity and temperature of the air, those very conditions which influence the transpiration of plants, are continually changing, this diversity is not really surprising. What endless series of gradations there are between the damp air of a tropical estuary, and the arid wastes in the interior of large continents! What varieties of temperature in the different zones and regions of the earth, and in the changing seasons; what differences, even in a narrow space in a single small valley, between the conditions of moisture of the air and ground in the depths of a shady glen, and on the sunny, rocky slopes! In the one place the air is so saturated with water-vapour that even evaporation cannot take place from exposed pieces of water, much less than from plants; in the other it is so dry and the sun is so strong that plants can hardly suck up enough from the ground to compensate for the water evaporated from their surface. In the former case contrivances must be devised which will promote transpiration as much as possible; in the latter, however, it is important that too much evaporation, which would cause the drying up and death of the plant, should be prevented.

One of the most important ways of increasing transpiration consists in the development of many cells whose surface is in contact to the greatest possible extent with the atmospheric air, and which are so organized that water in the form of vapour can be exhaled from them. Further, it is of importance that the access of air to these cells is not rendered difficult, and that as great a portion as possible of these cell-groups, which help in transpiration, are reached by the rays of the sun. It is only in the delicate-leaved mosses, which have no stomata, that the whole of the cells of a leaf, in contact with the air, give off unlimited water, in the form of vapour, directly to the atmosphere. In plants possessing leaves provided with stomata, the outer walls of the epidermal cells, which are directly in contact with the air, are almost always rather thicker than the inner and side walls; moreover, the outer wall is overlaid by the already repeatedly mentioned covering, termed "*cuticle*", through which water-vapour can pass only with difficulty. In tropical ferns, especially in the tree-ferns, which grow in narrow wind-sheltered ravines, traversed by streams of water, and which spread out their fronds in the still, damp, warm air, the outer walls are so thin and delicate, and are covered by a cuticle of

such tenuity, that if the humidity of the air sinks only a few degrees below saturation point, or if a transient sunbeam enters the ravine even for a short time, they immediately give off water-vapour.

Apart from such cases, the exhalation of water-vapour from the superficial cells is scarcely worth noticing; it is almost entirely restricted to the cells of the spongy parenchyma. Here are to be found, indeed, very striking arrangements, which must be regarded as contrivances for increasing transpiration. First of all, where transpiration is to be accelerated, the green, spongy tissue is very strongly developed, the air-containing lacunæ and passages, which penetrate the net-work of branched cells like a maze, are enlarged and numerous, and the collective free surface of all the air-bordered cells in the interior of the leaf has a much greater extent than the mere outer surface of the epidermis. In the leaves of many tropical plants which are always surrounded by damp warm air, e.g. in those of the Brazilian *Franciscea eximia*, of which a section is represented in fig. 62<sup>1</sup>, almost the entire thickness is made up of loose wide-meshed spongy parenchyma, and it is evident that water will be exhaled from the cells of this tissue as soon as the temperature of the leaf is raised even to the extent of a few degrees above that of the moist surrounding air by the sunbeams falling upon it.

In many such plants which urgently require a help to transpiration on account of their situation, the cavities of the spongy parenchyma are extraordinarily enlarged and widened at certain points where the greatest number of stomata are developed. The difference in appearance between such places and other parts of the leaf having dense spongy parenchyma can indeed be recognized by the unaided vision. In such a leaf looked at from above, the large-meshed portions of the spongy parenchyma appear as lighter spots in the dark-green grounding; the leaf is flecked and marked with white. This is not only the case with many plants of damp, tropical forests, but also in those of temperate zones, such as species of the genus *Cyclamen*, *Galeobdolon luteum*, the Lungwort (*Pulmonaria officinalis*), and frequently also in *Hepatica triloba*, if they grow in very shady places on the damp ground of a forest. It must, of course, not be forgotten that all the white spots and markings of green leaves, which have been named collectively "variegations", are not due to this cause. In those nettle-like plants, known as *Bæhmerias*, the white spots on the central part of the leaf lamina are caused by peculiar groups of crystals in the epidermal cells, the so-called *cystoliths*, which reflect the light; in some *Piperaceæ* they are due to groups of epidermal cells which are filled with air, and below which the palisade cells are absent; in other plants, again, they may be caused by the formation of aqueous tissue, a structure which will be discussed later. In many of those plants with variegated leaves, which are so extensively cultivated for purposes of decoration, the variegation is not normal, but must be considered as pathological, and is in no way connected with transpiration.

Since, as we know by experience, transpiration of green leaves is increased by light and warmth, it is evidently an advantage for all those plants to which only a restricted number of sunbeams can obtain access, if their leaf-blades are very large

and have such a form and position that the small supply of light can be utilized to the full. The resultant action is just the same whether 1000 green cells are only moderately illuminated, or if 500 cells are illuminated by a light twice as strong. If this argument will not apply to all plants, it certainly fully applies to some, and it is a fact that plants growing in damp, shady places are characterized by their comparatively large, thin, delicate leaves. These leaves are also spread out horizontally in such localities; they are smooth and not wrinkled; neither rolled back nor bent up. Suppose we enter a thick wood in the north temperate zone, perhaps in S. Germany. By the side of delicate-leaved ferns grow species of *Corydalis* (*Corydalis fabacea, solida, cava*), together with species of *Dentaria* (*D. bulbifera, digitata, enneaphyllos*), dog's mercury (*Mercurialis perennis*), *Isopyrum thalictroides*, bitter vetch (*Orobus vernus*), woodruff (*Asperula odorata*), *Lunaria rediviva*, herb Paris (*Paris quadrifolia*), cuckoo-pint (*Arum maculatum*), spurge-laurel (*Daphne Mezereum*), and many other species belonging to very different families, but all having the common characteristic of possessing flattened leaves and no covering of hairs. If a brook ripples through the shady wood, growing on its banks will be found the yellow balsam (*Impatiens nolitangere*), the broad-leaved garlic (*Allium ursinum*), *Streptopus amplexifolius*, and the butter-burr (*Petasites officinalis*), with its huge foliage, all again characterized by their large, smooth, flat leaves. In such places in S. Germany are generally to be found the largest leaves. Those of the butter-burr attain to a length of over a metre, and are almost a metre broad. The fronds of the common bracken-fern (*Pteris aquilina*) are equally large in such situations; and on the ground in damp, shady alder woods, growing in comparatively cold mountain glens, another fern (*Polypodium alpestre*) is to be met with, whose frond is  $1\frac{1}{2}$  metres long. But they only possess these extended leaves when growing in the situations described, in the damp air of cool and shady woods. One would expect that under similar conditions outside the wood, the leaves would exhibit a more luxuriant growth, and would attain to a still larger size in consequence of the influence of a higher temperature; but this is not the case. In the drier air and sunshine on the unshaded banks of a rivulet, the leaves of the butter-burr are scarcely half as large as those growing in the neighbouring cold shady glen, from whose dim light the brooklet flows out into the open country; and on sunny ground neither of the two above-named ferns will even approximately reach that size to which they grow when surrounded by the cold, damp air in the depth of the alder wood.

This difference in the relative size of the leaves of one and the same species, according as to whether they grow in sunny places in dry air, or in shady spots in damp air, is sometimes carried so far that the whole physiognomy of the plants becomes altered, and they might easily be thought to belong to distinct species. Thus species of *Convallaria Polygonatum*, growing in shady meadows watered by rivulets, show leaves at least three times as large as those which grow on the rich damp earth on the steep sides of rocks down which water rushes, where they are warmed by the sun all the day. This comparison might be illustrated by

numerous other plants of the flora of Central Europe, which are sometimes to be found in damp, shady woods, sometimes in sunny fields; but the above examples will suffice to demonstrate the fact that in shady places and damp air, in spite of the smaller amount of heat, and even when the humidity of the soil is less, the leaves will, notwithstanding, have a greater size than in sunny places where they are surrounded by a drier air.

An apparent exception is to be found only when these plants are situated above the tree-line in Alpine regions. On the sunny slopes of Monte Baldo, in Venetia, far above the wood-line, *Corydalis fabacea* grows with the same luxuriance as in the shady forests of the lower hilly regions; and on one place on the Solstein chain, in the Tyrol, at a height of 1800 metres above the sea, dog's mercury and *Galeobdolon luteum*, species of valerian, spurge-laurel, and ferns can be seen rising above the boulders with leaves as large as those growing in the shade of the woods below. But this exception, as stated, is only an apparent one. Where these plants flourish on Alpine heights flooded with light, the air is just as damp as in the depth of the woods 1000 metres lower in the valley. For weeks the mist sways like drapery around the heights, and the air, consequently, is certainly not drier than in the woods down in the valley. Indeed, the fact that plants, which one is accustomed to see inhabiting the shady woods in the depth of the valley, grow in Alpine regions on unshaded places with leaves of the same size and shape as before, is a proof that the large size of their leaves in the dark woods of these lower places is not due to the absence of light, but to the very moist condition of the air which prevails there. Plants, whether in the shade of the forests, or on the illuminated heights of the mountains, endeavour to compensate for the detrimental influence of the greater humidity of the air by the formation of an extensive transpiring surface.

So far the increase of leaf surface may be considered absolutely as a means of helping transpiration. This method of increasing transpiration comes into action in the tropics in a much more striking way than even in the temperate zones. Especially in the most characteristic plant-structures of the tropics may it be observed how intimately the size of the leaves corresponds to the conditions of moisture of the air, and how it is that palms develop the largest leaves just in those districts where, in consequence of the air being saturated with aqueous vapour, plants can only transpire with difficulty. In the dampest parts of Ceylon grows the gigantic *Corypha umbraculifera*. A copy of a drawing of this tree, sketched on the spot by Ransonnet, is given in fig. 63. It towers above the tops of all other plants, and its leaf-blades are from 7 to 8 metres long, and 5 to 6 metres broad. In similar situations in Brazil the palm *Raphia taedigera* spreads out its fronds like gigantic feathers. The petiole of this leaf alone is 4 to 5 metres long, and the green feather-like blade is from 19 to 22 metres long and 12 metres broad—the greatest extent which has hitherto been observed in any leaf. Others palms besides these giants, whose fronds wave all the year round in a damp atmosphere, are but little inferior to them. Under one leaf of the Talipot ten persons can easily find room and shelter, and if the pinnate leaves of the Sago-palm be imagined

propped up against the houses in the streets of our towns, their tops would reach to the second story, and it would be possible to climb up to the windows by them as if by the rungs of a ladder. Many of these palm leaves if placed in an upright position would be equal in height to our forest trees. In all these leaves the epidermis is only slightly thickened, the spongy parenchyma is well developed, stomata are present in large numbers, and the surfaces of the leaves are so directed towards the incident sunbeams that they are abundantly illumined and warmed throughout. The leaves become decidedly heated by the sun's rays, and thus, even in the saturated air of the tropics, the necessary amount of transpiration becomes possible. Arrangements similar to those of the palms may be observed in the Aroids and Bananas. These also develop their most extended leaves in the saturated or almost saturated atmosphere on the banks of still or flowing water, and in the moist heavy air of tropical primeval forests.

It is obvious that means of increasing transpiration are required in those water-plants whose roots are in the wet mud at the bottom of lakes and ponds, whose stems and leaf-stalks are directly surrounded by water, and whose leaf-blades float on the surface of the water, as for example the water-lilies (*Nymphaea*, *Victoria*), the Frogbit (*Hydrocharis morsus-ranae*), and the Nymphæa-like *Villarsia* (*V. nymphoides*). The blade of the leaf is disc-shaped in all these plants, and the discs lie side by side flat on the surface of the water. Frequently large areas of lakes and ponds are covered with the floating leaves of these plants. The whole of the upper side of such a leaf can receive the rays of the sun, and the leaf is thus warmed and illuminated throughout. The under side of the leaf is coloured violet by a pigment called *anthocyanin*, which we will consider more in detail later, and of which it need only be mentioned now that it changes light into heat, and thereby materially helps to warm the leaves.

The aqueous vapour which is in consequence developed cannot escape below from the large air-spaces which permeate the leaf, because the under side, which floats on and is wetted by the water, possesses no stomata. The upper side is so richly furnished with stomata that on 1 sq. mm. 460 are to be seen, and on a single water-lily leaf about  $2\frac{1}{2}$  sq. dms. in area, about  $11\frac{1}{2}$  millions. This upper side alone provides a means of exit, and it is therefore important that the passage should not be obstructed at the time of transpiration. If the rain should fall unrestrainedly on the upper side of the floating leaves, the collected rain-water might remain there for a long time, even while the sunbeams breaking through the clouds after the shower are warming the floating leaves and inciting them to transpire. In order to avoid this an arrangement is made by which it is rendered an impossibility to wet the upper side of the floating leaves. The falling rain is formed into round drops on reaching them, and does not spread over the leaf-surface so as to wet it. But in order that the drops should not remain long on the leaves in many of these forms, such as in the widely distributed water-lily (*Nymphaea alba*), the leaf, where it joins the stalk, is somewhat raised, and the edges are bent a little up and down in an undulating manner. This gives rise to very shallow depressions

round the edge of the disc, on account of which the drops of water roll down from the middle of the leaf to the edge on the slightest rocking movement, and there coalesce with the water on which the leaves float.

This puckering of the margin of the leaf is attended in the water-lilies by a phenomenon which, although not directly associated with the matter in hand, is so full of interest that it cannot be passed without notice. If we take a boat in the bright sunshine at mid-day, and float over the calm inlet of a lake, whose surface is overspread with the leaves of water-lilies, and if the water is clear to the bottom, we shall see the shadows of the leaves which float on the surface sketched out on the ground below. But we can scarcely believe our eyes—these do not look like the shadows of the leaves of water-lilies, but rather



Fig. 68.—*Corypha umbraculifera* of Ceylon (after Ransonnet).

of the fronds of huge fan-palms. From a dark central portion radiate out long dark strips which are separated from each other by as many light bands. The cause of this peculiar form of shadow is to be found in the undulating margin of the floating leaves. The water of the lake adheres to the whole of the under surface of the disc as far as the edge, and is drawn up by capillarity to the arched portions

of the undulating margin. The sun's rays are refracted as through a lens by this raised water, and so a light stripe corresponding to each convex division of the curved margin is formed on the bed of the lake, and a dark stripe corresponding to each concave part. These are arranged in a radiating manner round the dark central portion of the shadow.

#### MAINTENANCE OF A FREE PASSAGE FOR AQUEOUS VAPOUR.

Special arrangements are met with in all plants which possess stomata, in order that the giving off of aqueous vapour may continue without hindrance. Water falling on the upper side of the leaf, in the form of rain and dew, threatens to cause the greatest obstacle to this free passage should it be able to collect directly in the stomata. The width of an open stomate does not render the entrance of water by capillarity impossible. As long as light and warmth exercise their power, as long as the temperature in the neighbourhood of the spongy parenchyma is higher than that of the surrounding air, and water-vapour in consequence is produced in the spongy tissue and driven out with force from the stomata, such an entrance is indeed inconceivable. It is impossible for aqueous vapour to pass out and at the same time for fluid water to enter by the same passage and through the same gate. But should the leaf become cooled by radiation after sunset, and dew be deposited upon it, or should a cold rain trickle down over the leaves, and the stomata have been unable to close quickly enough, it is quite possible that water might enter, just as it enters a retort (whose narrow mouth dips into water, and whose contents have been vaporized by placing a lamp under them), when the lamp is removed, and the bulb of the retort with its contents becomes cooled. But putting aside the possibility of water thus pressing its way in, this much is certain, that the formation of a layer of water over the cells in the immediate neighbourhood of the stomata would cause great injury to the plants; and this, not only as affecting transpiration, but also the free entrance and exit of gases. Therefore, the immediate surroundings of the stomata must be kept open as a path for aqueous vapour, and no water must be allowed to collect and take up a position there.

Stomata are much too small to be seen with the naked eye. However, it can be ascertained by a very simple experiment whereabouts, on a leaf or green branch, stomata are to be found. A twig or a leaf is dipped in water, and then withdrawn after a short time and lightly shaken; some spots will be found wet, while other places remain dry. Where water remains and spreads out to form an adhering film, no stomata will be found in the epidermis; but where the twig or leaf is dry, one can be sure of finding them. In 80 per cent of cases experimented upon in this way, only the upper leaf-surface became wetted, while the under side kept dry; in 10 per cent both sides remained dry; and in the other 10 per cent the upper side kept dry, while it was the under side which was wetted. With this corresponds the actual fact that in far the greater number of instances the under side possesses most stomata, while the upper side is free from them. It seems as if

this circumstance could be explained thus, that the upper side is usually turned towards the rain, and that the stomata are on this account collected together on the under side, which is sheltered from it. This explanation, however, which at first sight seems so plausible, does not quite correspond to the true state of the case. The consideration of the reasons for believing that it is an advantage for the plant to have the upper side of the leaf free from stomata will indeed come later, but one thing must be noted here,—that the side of the leaf turned towards the ground, which in most cases contains all the stomata, remains anything but dry. Of course the rain-water only reaches the surface of the horizontal leaf-blade when the margin is so formed that the adherent layer of water which wets the surface is drawn over gradually from the upper to the under side, and that is very seldom the case; but the wetting of this surface by mist and dew is all the more important on this account. On taking a stroll through fields and meadows on a dewy morning, as a rule only the upper surfaces of the leaves come into view, and one might easily be led to think that the dew is deposited only on this side. We constantly use the expression that the dew "falls". Underlying this is the idea that the dew comes down like rain, and that only the upper leaf-surface becomes covered with dewdrops. But one has only to turn the leaf over to convince oneself that the lower surface is likewise bedewed, and on a closer examination it will even be seen that dew is of more importance in connection with the lower than the upper side, because it remains there so much longer. When the sun is already high in the heaven, and the dewdrops have long disappeared from the upper surface, and transpiration is in full force, the under side may still be found studded with dewdrops. If in the majority of cases the stomata lie on the under side, and this side is exposed to the danger of being covered with water as much as the upper one, it is evident why contrivances for hindering the access of water to the stomata are to be found much more abundantly on the under than on the upper side of the leaf.

The most important of these arrangements are the following:—

First the *coating of wax*. This is either in the form of a granular covering; or as a fine crust which fits closely to the epidermis; or, most commonly, as a continuous thin layer which is easily rubbed off, forming a delicate film popularly known as "bloom". A group of primulas, belonging to mountainous districts and to the moors of low countries, of which *Primula farinosa* may be taken as the most widely distributed and best known representative, have a rosette of leaves spreading over the damp ground, and on the lower side of these leaves is a white coat, which under the microscope is seen to consist of a collection of short rods and knobs of a waxy nature. If such a leaf is plucked and placed in water for a short time, and then withdrawn, the upper side, which is quite free from stomata, will be moistened by a layer of water, while the under side, on which are the stomata protected by the granular coating of wax, remains quite dry. The lower surface of the leaves is covered with a fine closely adherent wax layer, in many of the willows growing in damp misty places near rivers (*Salix amygdalina*, *purpurea*, *pruinosa*), as well as

in a great number of rushes, bulrushes, and reed-like grasses. If when the dew falls heaviest one roams through a thicket of willows, or across a moor, one may see plenty of drops hanging from the under side of the leaves, but they do not actually wet this surface, and on the slightest movement of the leaves they roll off and fall down. It is, indeed, in consequence of this that one is more likely to get thoroughly wet by walking through meadows and dwarf willows than by an excursion through country overgrown with ordinary herbs. The two white stripes, so well known on the under side of fir leaves, are also formed by a waxy coat, which prevents the stomata below from being wetted. In species of juniper (e.g. *J. communis*, *nana*, *Sabina*) the two white stripes occur on the upper side of the leaf, and it is interesting to see how the distribution of the stomata again corresponds; for junipers belong to that group of plants whose under leaf-surface is free from stomata, these being present only on the wax-coated region of the upper side of the leaves. Many grasses, to which we shall refer later for other reasons (e.g. *Festuca punctoria*), only possess stomata on the upper side of the leaf, and again only where the strips of wax are situated. Generally speaking, wax is a protection from moisture, and is most frequently formed when the stomata make their appearance on the upper side of the leaf. The leaves of peas, nasturtiums, woodbine, poppies, fumitory, many pinks, cabbages, woad, and many other cruciferous plants, which have stomata on the upper surface, also produce a covering of wax there. Water poured on the upper surface of a cabbage-leaf rolls off in the form of drops, exactly as it runs off a duck's back, without wetting the surface. In the fronds of ferns (e.g. *Polypodium glaucophyllum* and *sporocarpum*), on the upright leaves of Irises (*Iris germanica*, *pumila*, *pallida*), as well as on the vertical leaves and leaf-like branches of many Australian acacias and myrtles, and lastly in the erect whiplike, leafless or scantily-leaved papilionaceous plants (*Retama*, *Spartium*), the stomata are protected from the wet by a coat of wax.

The formation of *hairs* furnishes another barrier to the entrance of water into the stomata. We shall come back again to these structures, which serve so many different purposes in the plant economy, but here only those hairy and felted coverings whose task is to hinder the wetting of the stomata will be considered. Examples of these are furnished by many Malvaceæ which grow in marshes and ditches (e.g. *Althaea officinalis*), and also by some mulleins (e.g. *Verbascum Thapsus*, *phlomoides*), whose leaves are provided with stomata on both surfaces, and with hairy coverings which it is impossible to moisten. In the damp meadows of the valleys of the Lower Alps grows *Centaurea Pseudophrygea*, whose large leaves, hairy on both sides, are very rough and much wrinkled. The stomata are only situated in the hollows between the ridges. When rain falls, or the leaf becomes bedewed, the water remains in the form of drops on the hairs of the elevated portions, and the cells in the hollows are not wetted. In many alpine plants, for example the Hairy Hawkweed (*Hieracium villosum*), after a fall of rain or dew the long projecting hairs of the leaves are thickly beset with drops of water, none of which can reach the stomata on the epidermis beneath.

It should be particularly noticed here that plants with two-coloured leaves, such as those whose upper surfaces are green, smooth, free from stomata and easily wetted, while their under surfaces, covered with gray or white hairs, and rich in stomata, which cannot be wetted, are generally to be found on the banks of rivers and streams.

In the open woods which skirt the banks of rivers in the valleys of mountainous districts, *i.e.* in places where mist rises on summer evenings, and all the twigs, leaves, and stalks are covered with drops of water, the most characteristic plants are the Gray Alder (*Alnus incana*) and the Gray Willow (*Salix incana*), and as undergrowth everywhere the Raspberry—all plants adorned with the two-coloured leaves just described. Leaving the region of woods growing on river banks for the neighbouring meadows, through which ripples fresh water from a spring, and where everything drips with dew from evening until the middle of the following day, we come to the natural home of herbs and shrubs with leaves green on the upper and white on the under sides. There Fuller's Thistles (*Cirsium heterophyllum* and *canum*) grow luxuriantly, and the Meadow-sweet, with its large two-coloured leaves; whilst the whole course of the brook is bordered by the Colt's-foot (*Tussilago Farfara*) with leaves which may be considered typical of this group.

What a contrast does this present to the lofty vaults of a dense forest, perhaps only a thousand paces away, where on the shady ground little or no dew is formed, and where the leaves which canopy the brown soil are never exposed to a thorough wetting! No parti-coloured leaf is to be found there, no leaves whose upper surface is green and smooth, while the under side is covered with white hairs; and plants which exhibit a thick coating of wax on their under surface, like the *Primula farinosa* of the moors, are also absent. On the other hand ferns are here, as for example the Hard Fern (*Blechnum Spicant*), whose leaves are furnished with stomata which open quite without protection on the tops of projecting undulations. This contrast between the leaves of plants in the open marshy country and in the interior of forests is found, not only in the colder territories of the north, but also in tropical districts. Moreover, plants whose leaves are covered with white hairs on the under surface are never to be found under the close leafy roof of huge trees which prevent nocturnal radiation and the formation of dew. Here occur, rather, plants having totally unprotected stomata opening on slightly raised areas of the surface, as for example in *Pomaderis phyllicifolia*, and on the leaves of the Pepper family, *e.g.* *Peperomia arifolia* (see fig. 64<sup>3</sup> and 64<sup>4</sup>).

A very remarkable contrivance by which stomata are protected from moisture consists in providing the stomata of the upper surface with countless papillæ and cone-shaped projections; between them, of course, being innumerable hollows and depressions. Falling water-drops roll off such surfaces; the water cannot displace the atmospheric air in the depressions, and therefore the leaves and stems, in so far as their epidermis presents the aforesaid irregularities, appear covered with a thin layer of air. As the stomata are situated in the small hollows, they always remain

dry, and even if that particular part of the plant is wholly immersed, they do not come into contact with the water. There are two causes for the unevenness of the leaves: first, the outer walls of a portion of the superficial cells may become strongly arched outwards; or secondly, solid peg-like projections may arise from the cuticle, and to these projections the air adheres so firmly that it cannot be displaced even by a considerable pressure of water. This protection of stomata against moisture by papilla-like outgrowths is to be found especially in marsh plants which are exposed to a changing water-level. On the banks of streams and rivers, and

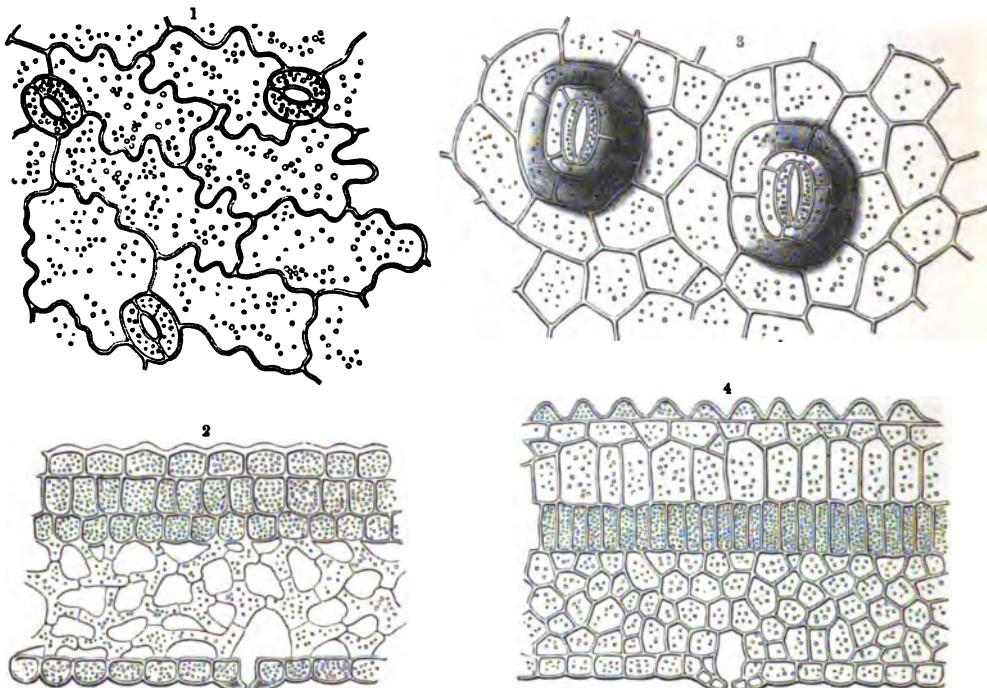


Fig. 64.—Stomata.

<sup>1</sup> Surface view of a portion of the frond of the fern *Nephrodium Filix-mas*. <sup>2</sup> Vertical section through this portion.  
<sup>3</sup> Surface view of a portion of the leaf of *Peperomia arifolia*. <sup>4</sup> Vertical section through this portion;  $\times 350$ .

where water welling up from below forms pools and ponds, it may happen that plants are submerged for a week at a time, and then again remain dry for some months.

Most of the plants growing in such situations, particularly the sedges (e.g. *Carex stricta* and *paludosa*), the rushes (e.g. *Scirpus lacustris*), most of the tall fistular grasses (*Glyceria spectabilis*, *Phalaris arundinacea*, *Eulalia japonica*), the plants which grow with the sedges (e.g. *Lysimachia thyrsiflora*, *Polygonum amphibium*), and many other marsh plants, are all saved from the danger of having their stomata wetted during their submersion by the papilla-like outgrowths of some of the epidermal cells, near the stomata, as shown in the figures on next page.

Bamboos, and the grasses *Arundinaria glaucescens* and *Phyllostachys bam-*

*bisoides*, which so much resemble the bamboos, besides some sedges (e.g. *Carex pendula*), exhibit on the other hand the above-named peg-like projections of the cuticle; these are shown in the section of a bamboo leaf in fig. 66<sup>2</sup>). On plunging such a bamboo leaf in water, a surprising sight presents itself. The upper side, covered by a dark green, smooth, flat epidermis, with no stomata, becomes wet all over, and retains its dark colour and dull appearance; but the under surface, blue-green in colour, and beset with stomata and thousands of cuticular pegs, does not allow the air to be displaced; and this layer of air, spread thin over the surface, glistens under water like polished silver! The leaf may be shaken under water to any extent, and may even be left submerged for a week, but the silvery glistening air-stratum is not dislodged. If such a leaf is now taken out of the water, the upper surface is quite wet, but the under surface is dry, like a hand which has been dipped in mercury and then withdrawn, and not the smallest drop of water

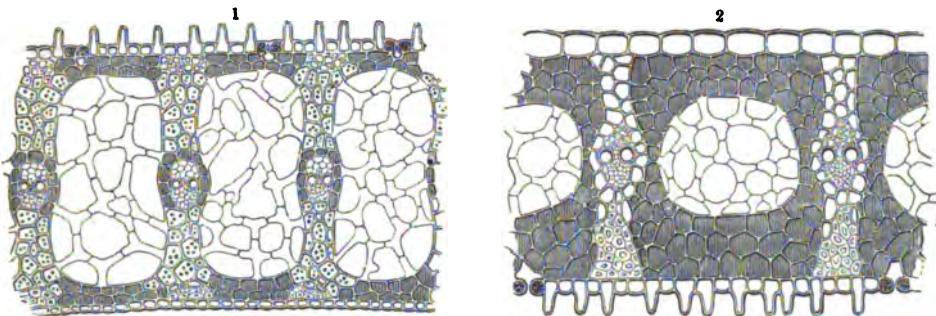


Fig. 65.—Protection of Stomata from Moisture by Papilla-like outgrowths of the Surface.

<sup>1</sup> Vertical section through a portion of the leaf of *Glyceria spectabilis*. <sup>2</sup> Vertical section through a portion of the leaf of *Carex paludosa*;  $\times 200$ .

adheres to it. On placing a vessel of water, in which some bamboo leaves are half immersed, under the receiver of an air-pump, and then pumping out the air, numerous small air-bubbles are at once given off from the submerged portions of the leaves. At length the silvery lustre disappears, and the air between the cuticular pegs is replaced by water. If now the leaves be completely submerged, the silver lustre is only shown on those parts which were not previously immersed, and where water could not replace the exhausted air;—the spaces round the pegs in this region having been again supplied with air on the opening of the stop-cock of the pump in order to submerge the leaves. It may be imagined from this experiment how much the stomata would be damaged by water if the plants mentioned were not protected from moisture by the pegs to which the air adheres so strongly.

In many plants which grow in the sunshine, and particularly in those whose foliage is evergreen and only exposed to moisture at the time of the greatest activity of the sap (while later it is exposed for months to dry air), the stomata are to be found surrounded by an embankment, or sunk in special pits and furrows. Even in the leaves of many indigenous plants, which are green in the summer, e.g. those of the Carrot (*Daucus Carota*), the guard-cells of the stomata are so

over-arched by the neighbouring epidermal cells that a sort of vestibule is formed in front of the true pore. It can easily be imagined that drops of water which come to such places are not able to press out the air from this vestibule, and therefore cannot penetrate to the guard-cells of the stomata. In *Hakea florida* and *Protea mellifera*, two Australian shrubs (see fig. 67), similar arrangements are met with, but here the stomata are still more over-arched, so that they are only visible to anyone looking at the surface of the leaf through small holes at the top of the dome. The stomata on the green branches of various species of *Ephedra* are surrounded by mound-like projections from the cuticle of neighbouring epidermal cells, and are at the same time somewhat sunken, so that an urn-shaped space is

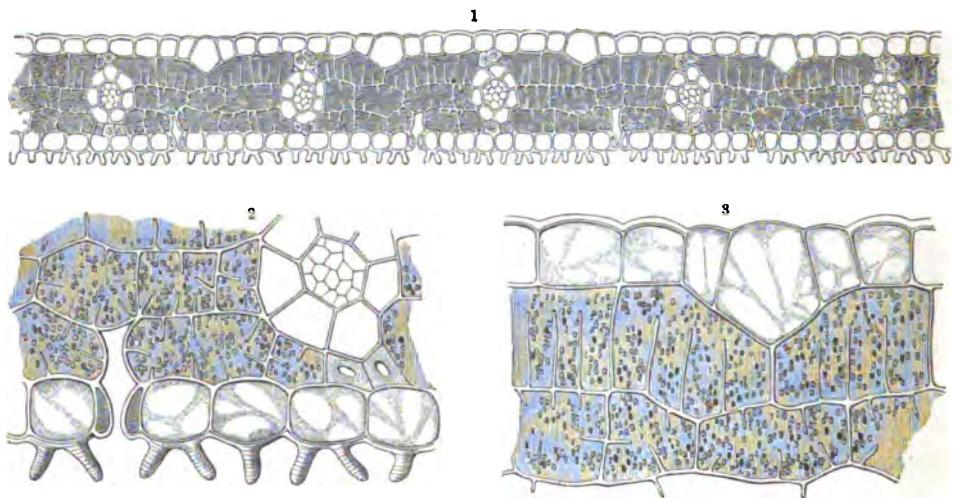


Fig. 66.—Protection of Stomata from Moisture by Cuticular Pega.

<sup>1</sup> Vertical section of a Bamboo leaf;  $\times 180$ . <sup>2</sup> Part of the lower portion of the section;  $\times 460$ . <sup>3</sup> Part of the upper portion of the section;  $\times 460$ .

formed above each stoma, from which water cannot dislodge the air. On the leaves of *Dryandra floribunda*, one of the Proteaceæ which grows in the thick Australian bush, several stomata occur at the bottom of small pits on the under side of the leaf, and from the side walls of the depression spring hair-like structures which interlace and form a loose felt-work, easily penetrated by gases but not by fluids (fig. 68). The stomata on the leaves of the Oleander (*Nerium Oleander*) are similarly situated. These also are at the bottom of deep pits on the lower side of the leaf, and the entrance to them is beset with extremely delicate hair-like structures (see fig. 73<sup>3</sup>). The oleander fringes the banks of streams in the sunny open country of Southern Europe and the East, and in its natural position it is most exposed to wetting by rain, mist, and dew, just when transpiration is an absolute necessity for it. But even when the leaves are covered on both sides with a layer of moisture, none can force its way into the hair-lined depressions which conceal the stomata, and consequently transpiration is not hindered even in the wettest season of the year.

Stomata, which are spread over the green tissue of stems and flattened shoots, are frequently sunk in furrows, channels, and pits, in plants whose greatest activity occurs in the short rainy season, and they are saved from wetting in this position by the most varied contrivances. On the rocky shores of Lake Garda, and up over the mountain slopes to the heights of Monte Baldo, grows *Cytisus radiatus*, a shrub of unusual appearance (see fig. 69<sup>1</sup>). Its branches only possess rudimentary green leaves, and are themselves furnished with green tissue, which plays the same rôle as that assigned to the mesophyll of the leaf-lamina in normal foliaceous plants.

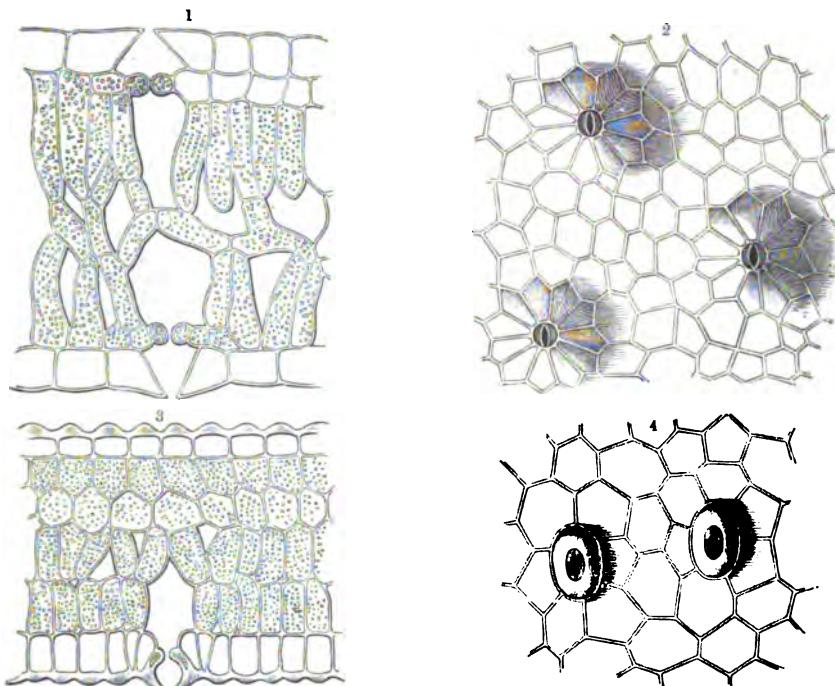


Fig. 67.—Over-arched Stomata of Australian Proteaceae.

<sup>1</sup> Vertical section through a leaf of *Hakea florula*. <sup>2</sup> Surface view of the same leaf;  $\times 320$ . <sup>3</sup> Vertical section of a leaf of *Protea mellifera*. <sup>4</sup> Surface view of the same leaf;  $\times 360$ .

These green branches bear very numerous secondary branches inserted in decussating pairs. On the secondary branches new shoots develop every spring exactly similar in form, and arranged in the same manner. At the period when this development is taking place, the humidity in that part of the Southern Alps, to which Monte Baldo belongs, is very great. In dull weather, rain and mist, or dew in fine weather, deposit large quantities of water on the soil, and on the plants covering it, particularly in the alpine region of the above-named mountains, on the westerly slopes leading down to the lake, which are thickly clothed with the shrubs in question. It is therefore important that the rod-like branches of this *Cytisus* should be able to breathe and transpire without hindrance, and that the short time during which the conditions for these vital transactions are favourable, should be fully and wholly taken advantage of. Here again the point above all others to be

aimed at is to keep a free passage for the water-vapour which must escape from the stomata. To bring this about, the stomata are situated in grooves filled with air which are sunk in the green tissue, and which give a striped appearance to the branches. Water cannot force out the air from these narrow furrows which run along the green branches and twigs, six of them to each branch. The branches may remain submerged in water for an hour without a trace of moisture entering the furrow. Moreover hairs are present in the furrows as a guard against moisture. These cannot be wetted, and the air adheres to them just as to the cuticular pegs of the bamboo leaf. A clear idea of this arrangement is given in the transverse section of the stem shown in fig. 69<sup>3</sup> and 69<sup>4</sup>. The adjacent section of the green branch of the Australian *Casuarina quadrivalvis* shows that these curious plants also have exactly the same arrangements, that the stomata lie at the bottom of

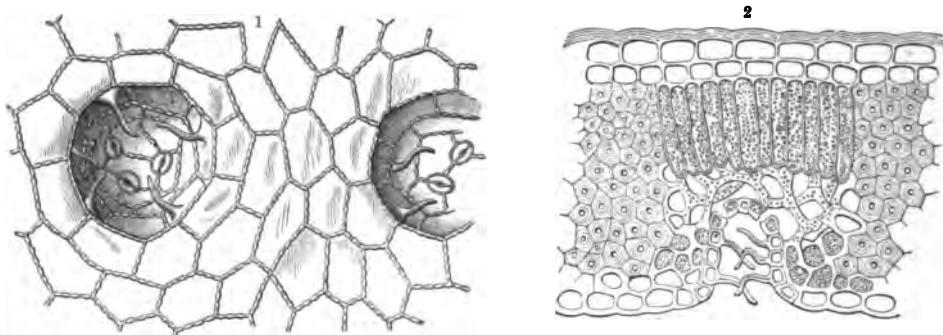


Fig. 68.—Stomata in Pit-like Depressions.

<sup>1</sup> Surface view of a leaf of *Dryandra floribunda*. A portion of the hairs which fill the pit is removed, in order to show the stomata;  $\times 350$ . <sup>2</sup> Vertical section through a leaf of *Dryandra floribunda*;  $\times 300$ .

narrow furrows which run along the green leafless branches, and that peculiar hair-structures are present in the furrows, to which the air adheres, forming a barrier against water, exactly as in those of the *Cytisus*. The Casuarinæ, which must finish their work for the year during the very short rainy period of their native country, require during this time arrangements providing for unhindered transpiration no less than does the *Cytisus* in the Southern Alps. Altogether this contrivance is found to be present in only a limited number of cases; in perhaps only twenty papilionaceous shrubs, most of which belong to the Spanish flora, of the genera *Retama*, *Genista*, *Ulex*, and *Sarrothamnus*, in addition to the Australian Casuarinas, and in allied species of *Cytisus* (*holopetalus*, *purgans*, *ephedroides*, *equisetiformis*, *candicans*, *albus*, &c.). Most remarkably also this arrangement occurs in a small species of Broom (*Genista pilosa*), which is distributed over the mountains of Central Europe, over the heaths of the Baltic Lowlands, Denmark, Belgium, and England. And the presence of this contrivance here is the more strange, from the fact that the green branches with their furrows, in which lie stomata, are not leafless, but, on the contrary, are provided with a comparatively well-developed foliage.

Among the most peculiar plants whose stomata are concealed in hidden nooks,

impenetrable by water, are two very small orchids, of which one, *Bolbophyllum minutissimum*, grows in company with mosses on blocks of sandstone and on the bark of trees in the rocky ravines near Port Jackson, and on the Richmond River on the east coast of Australia; the other, *Bolbophyllum Odoardi*, lives in similar

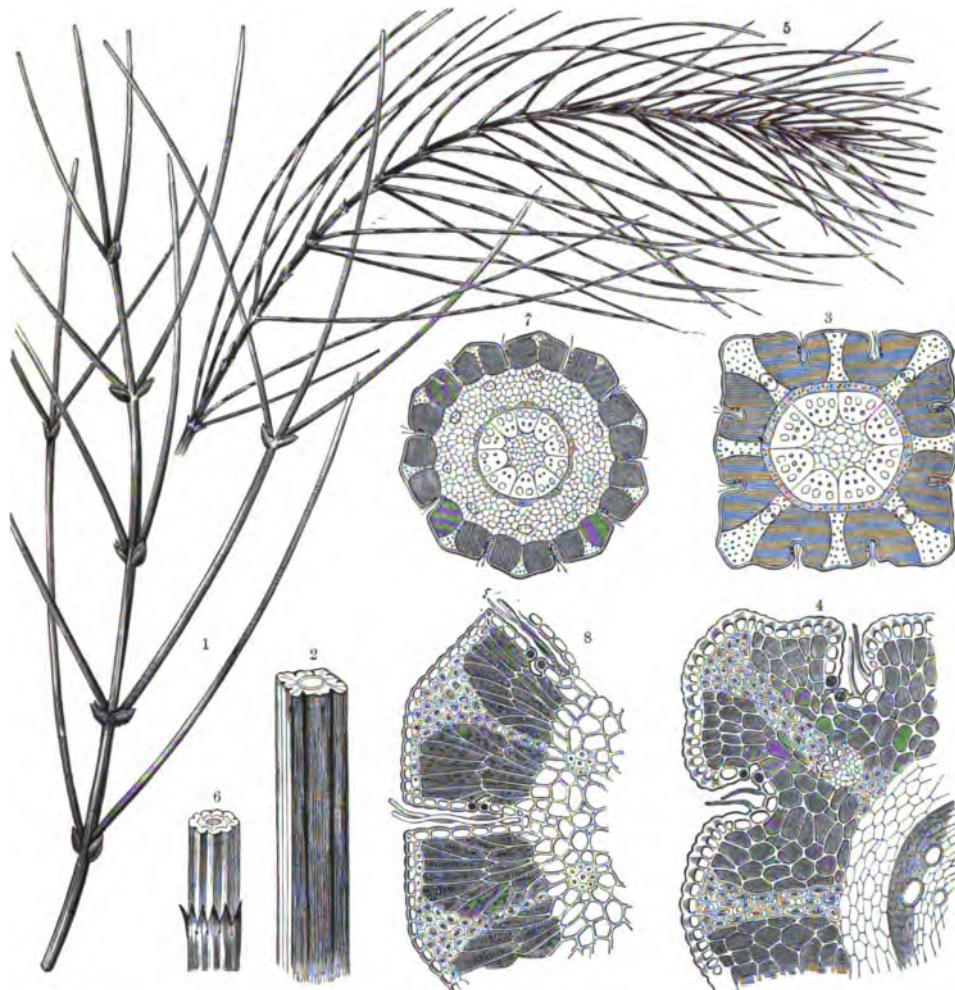


Fig. 69.—Stomata in the Furrows of Green Stems.

<sup>1</sup> Branch of *Cyrtus radiatus*; natural size. <sup>2</sup> Portion of a branch;  $\times 10$ . <sup>3</sup> Cross section of this branch;  $\times 30$ . <sup>4</sup> Part of the same section;  $\times 150$ . <sup>5</sup> Branch of *Casuarina quadrivalvis*; natural size. <sup>6</sup> Portion of a branch;  $\times 8$ . <sup>7</sup> Cross section of this branch;  $\times 30$ . <sup>8</sup> Part of the cross section;  $\times 130$ .

situations in Borneo. Both have a filamentous rhizome from which spring rootlets (from 2 to 5 mm. long and 0.3 mm. thick), arranged in pairs, by which they attach themselves to the stone and the bark of trees. Above the origin of each pair of rootlets is a little disc-shaped tuber, from  $1\frac{1}{2}$  to 3 mm. in diameter, and  $\frac{1}{2}$  mm. thick, with an aperture on the upper surface, scarcely  $\frac{1}{10}$  mm. broad, leading into a hollow chamber within the disc-shaped tubers, about 0.5 mm. broad and 0.1 mm. high (see figure 70). The leaves of *Bolbophyllum minutissimum* are reduced

to tiny pointed scales about  $\frac{1}{2}$  mm. in length; two of them are situated at the mouth of each cavity, and are inflected towards one another across it. In *Bolbophyllum Odoardi*, each of the small tubers bears only one small green leaf, which is about  $1\frac{1}{2}$  mm. long and 1 mm. broad, and is placed close to the opening of the chamber (see fig. 70<sup>4, 5, 6</sup>). Stomata are found exclusively in the interior of the hollow tubers. Water cannot enter through the narrow mouth into the air-containing chamber, and even when, in the rainy season, the whole of the mossy carpet, in which these smallest of all orchids are interwoven, is saturated with water, their transpiration continues unhindered, provided that the other conditions on which it depends are fulfilled. It is obvious that these structures which prevent moisture reaching the stomata during the wet season of the year can take on another function

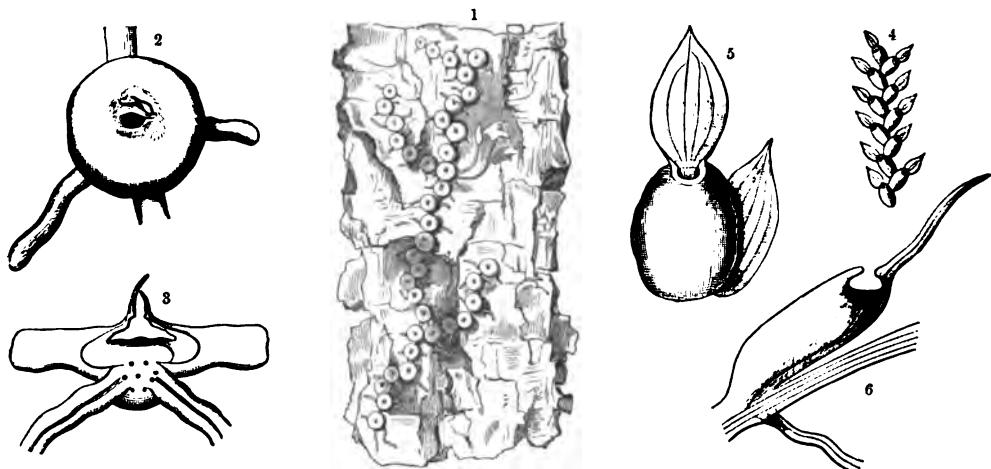


Fig. 70.—Orchids whose Stomata lie in Hollow Tuberules.

<sup>1</sup> *Bolbophyllum minutissimum*. <sup>2</sup> A tuber seen from above;  $\times 8$ . <sup>3</sup> Vertical section through this tuber;  $\times 15$ . <sup>4</sup> *Bolbophyllum Odoardi*. <sup>5</sup> A tuber;  $\times 6$ . <sup>6</sup> Longitudinal section through this tuber;  $\times 6$ .

in a succeeding dry period, which may follow immediately; but this must be spoken of again later.

The occurrence of "rolled leaves", which are observed in so many plants of widely different affinity, is also connected with the keeping of water from the stomata. The rolled leaf is always undivided, of small area, generally linear, but sometimes ovate-linear, elliptical, or even circular in outline; always stiff, and usually evergreen, and therefore living through two or three periods of vegetation. Its edges are bent down and more or less rolled back, even whilst still hidden in the bud. In consequence of this, the lower side which faces the soil is hollowed to a greater or less extent, while the upper side, turned skyward, is arched. Frequently the leaf is rolled so as to inclose an actual chamber, which only communicates with the outer world by a very narrow fissure, as is the case, for example, in the Crowberry (*Empetrum*). The rolled-back margins of the leaves in this plant almost touch one another, and the epidermis of the lower side of the leaf forms the actual lining of the cavity which resulted from the rolling of the leaf (see fig. 71<sup>2</sup>).

If the bent-back margins do not fit so closely together, a groove appears on the under side of the leaf, which is more or less sunken according to the extent of the rolling, as for example in the Heaths (*Erica caffra*, *vestita*, &c., see fig. 71<sup>1</sup>). Occasionally a groove is developed which divides into two side furrows running

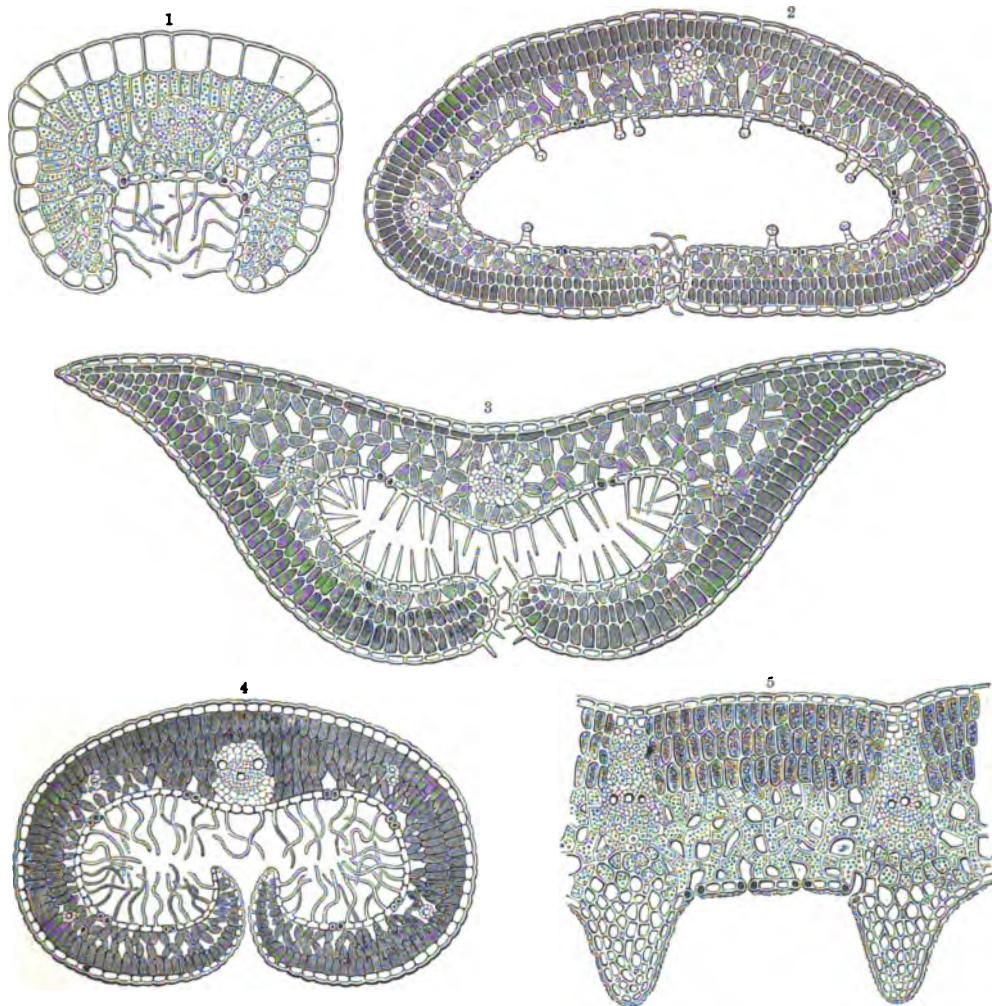


Fig. 71.—Transverse Sections through Rolled Leaves.

- <sup>1</sup> *Erica caffra*;  $\times 280$ . <sup>2</sup> *Empetrum nigrum*;  $\times 160$ . <sup>3</sup> *Andromeda tetragona*;  $\times 150$ . <sup>4</sup> *Tylanthus ericoides*;  $\times 130$ .  
<sup>5</sup> *Salix reticulata*;  $\times 200$ .

beneath the rolled edges, as for example in the leaves of *Andromeda tetragona* (fig. 71<sup>3</sup>), and in those of the Cape Rhamne, *Tylanthus ericoides* (fig. 71<sup>4</sup>). The central portion of the space framed in by the rolled-back leaves is also frequently divided into two longitudinal grooves, and in such a manner that the tissue below the midrib of the leaf may project as a broad strong band. On the under side of the leaf, therefore, are three longitudinally elongated parallel projections, a central one under the midrib, and two lateral, which have been formed by the rolled-back margins

of the leaf. On the right and left of the middle ridge lie two deep grooves, which are apparent to the naked eye as light stripes between the dark green projecting portions. This is the case, for example, in the leaves of the *Azalea procumbens*, also in one of the Ericaceæ known by the name of *Loiseleuria*, which covers the soil with a close-matted carpet wherever it makes its appearance, and is widely distributed through Labrador, Greenland, Iceland, Lapland, and generally through the whole Arctic region, as well as over the high mountains of Scandinavia, the Pyrenees, Alps, and Carpathians. The annexed figure 72 represents a transverse section through a single rolled leaf of *Azalea*, a hundred and forty times its natural size.

Occasionally several strong anastomosing ribs project from the under side of the rolled leaf, inclosing small pits and depressions in whose depth stomata are situated, as may be seen in the leaves of the widely distributed Willow, *Salix reticulata* (see fig. 71<sup>5</sup>).

Although all these rolled leaves have an appearance of firmness and solidity, and frequently remind one of the needle-like leaves of the conifers, they are, unlike these, filled up with a very loose spongy parenchyma, which takes up far more room than the palisade tissue lying beneath the epidermis of the upper side. The upper epidermis of all rolled leaves is easily wetted, frequently uneven and finely wrinkled, destitute of any waxy covering; the cells strongly thickened on their outer walls, and pressed closely together, so as to leave no spaces between them. On the under side it is very different. Here stomata are present in great number, and the epidermis is either covered with wax, as in the Marsh Andromeda, the Whortleberry, and the Reticulate Willow (*Andromeda polifolia*, *Oxycoccus palustris*, and *Salix reticulata*), or it is clothed with a fine felt-work, as, for example, in *Ledum palustre*. Very often peculiar rod-shaped or filamentous projections of the cuticle are present, which at first sight might be taken for hairs, but which differ from hairs in being solid, not hollow. Figs. 72 and 71<sup>1, 2, 3</sup> show these structures (which may be considered as counterparts of the cuticular pegs on the bamboo leaf) on the under side of *Azalea procumbens*, *Erica caffra*, and *Andromeda tetragona*, as well as on the edges of the fissure which leads into the hollow leaf of the Crowberry (*Empetrum nigrum*). These structures are to be found almost without exception in the heathers of the northern moors as well as in the Mediterranean and Cape flora. The importance of this continuous delicate coat lies chiefly in the fact that air adheres to it as to the cuticular pegs of the bamboo leaf, and indeed so firmly that even water, under considerable pressure, is not able to displace it. On placing a leaf of *Azalea procumbens* under water, two elongated air-bubbles are seen along the two longitudinal furrows, which glisten like two strips of silver. Even shaking the leaf to and fro will not dislodge these air-vesicles, and even if the branch has been left submerged for a week, this air will still cling to the depressions in whose depths the stomata occur. If the branch be removed from the water it will be seen that the upper side of the leaves is wet, while water has been kept away from the stomata of the under side. And as with *Azalea procumbens*, so is

it with all other rolled leaves, whether they belong to Cape plants or to heath plants of the Baltic lowlands.

It cannot be doubted that the mechanism of rolled leaves, as just described, furnishes a protection for the stomata against moisture, and keeps open a passage for aqueous vapour and excreted gases. The question is now only how it comes about that this arrangement is to be met with in plants of such widely distant countries and under such differences of climate?

In order to understand this clearly, let us imagine ourselves in some of the regions which are specially characterized by the abundance of plants with rolled leaves. First, on one of the high ridges of the Central Alps, where the low-lying *Azalea* spreads a thick covering over the soil, where *Erica carnea* in great quantity

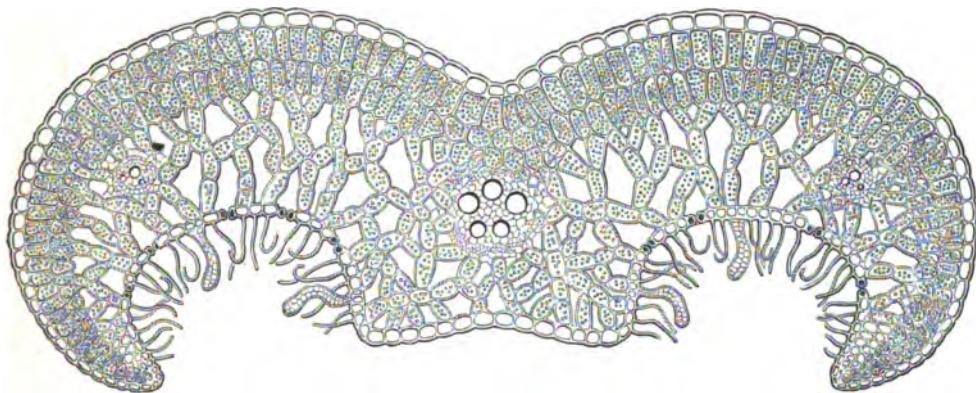


Fig. 72.—Vertical Section through a Rolled Leaf of the Trailing Azalea (*Azalea procumbens*);  $\times 140$ .

covers broad slopes, where *Dryas octopetala*, *Salix reticulata*, *Homogyne discolor*, *Saxifraga cæsia*, and many other plants which possess evergreen rolled leaves weave their carpet over the stony earth. The ground in which all these plants are rooted, and from which they draw their fluid nourishment, has many natural dikes and retains a large quantity of water, not only from the melting of the heavy winter mantle of snow, but also from the abundant rain of summer. For weeks together the heights are wrapped in a cold mist which saturates everything with moisture, and drops of water hang from the stems and leaves, unable to evaporate as long as the air remains so supercharged with vapour. At length the sky clears again, and the water on the plants begins to disappear. But even during the fine night following, all the plants become covered with a very heavy dew in consequence of their rapid cooling and radiation, and this not unfrequently remains until the middle of the next day. Transpiration at last occurs when the sun shines, and particularly if dry winds sweep over the heights. But who knows how long this state of things will continue? Each moment is precious, and every hindrance to the evaporation, so important for the plants, would be a distinct disadvantage. The outlets for aqueous vapour on the under side of the leaves especially should not be obstructed, and the above described contrivance is arranged with this end in

view. It can hardly be doubted that the earlier mentioned plants of high mountainous regions cease to transpire for weeks at a time in the wet seasons, when a thick unbroken mist covers the slopes, and earth, stones, and vegetation are dripping with moisture; and of course the conduction of food-salts to the green leaves is interrupted to a corresponding extent. If one considers how short a period is afforded to plants of high mountain districts in which to perform their year's work, it will be understood how the most active means for promoting transpiration must be brought into play, and how everything which might interrupt or limit this process, so important to the welfare of the plant, must be avoided. A few months after the last snow has melted on the heights, fresh snow again falls, and entirely prevents growth and nourishment during the long winter.

These climatic conditions account for the fact that so many Alpine plants, almost all those having rolled leaves, are evergreen. It is necessary that every sunbeam during the short vegetative period should be utilized, and that the leaves retained from the previous year should be able to transpire and to form organic materials on the first sunny day after the winter snow has melted, although the soil may have become only slightly warmed. It may perhaps be urged against this explanation that though, in the steppes the period of vegetation is restricted to the brief space of three months, nevertheless evergreen plants with rolled leaves are completely absent. But the conditions of moisture on the steppes during this three months' vegetative period are essentially different from those of the high mountain region. In the steppes, transpiration is never brought to a temporary standstill by too much moisture; evaporation can take place uninterruptedly from the leaves, and they have to be protected not from moisture, but from over-transpiration. With the exception of the halophytes and a few other growths which are particularly well protected, no plants, on account of the extreme dryness of the air, can retain their green foliage in the height of summer on the steppes.

Some of the plants which adorn the high mountains of southern regions make their appearance in the lower plains of the extreme north. The same carpet of Trailing Azalea, Dwarf Willows, and Dryas (*Azalea procumbens*, *Salix reticulata*, *Dryas octopetala*) is found on the soil underfoot. In addition are other small plants which remain green during the winter (e.g. *Cassiope tetragona*), which are similarly provided with rolled leaves. Even if we were not informed by Arctic explorers that the number of foggy days in the course of the short Arctic summer is much greater than on the mountain heights of the south, and that therefore a help instead of a hindrance to transpiration is required, the utmost use being made of the short time in which it is possible to draw food-salts from the soil, we might infer this to be the case from the frequent appearance of these small carpet-forming plants with their evergreen rolled leaves. Apart from other considerations, and disregarding the development of the various floral areas in point of time, the above signification of the evergreen rolled leaves explains the similarity and partial identity of the arctic flora with that of the heights mentioned.

Let us turn now to the low-lying country along the North and Baltic Seas, and

to the lowlands, which extend as far as the northern slopes of the Alps. Where man has not transformed the ground into arable soil, only moor and heath, heath and moor, are seen in wearisome monotony. On the moors especially are always the same plants—various Heaths (*Calluna vulgaris*, *Erica Tetralix*, *Erica cinerea*), Black Crowberry (*Empetrum nigrum*), Whortleberry (*Oxycoccus palustris*), Marsh Andromeda (*Andromeda polifolia*), Wild Rosemary (*Ledum palustre*)—all plants with evergreen rolled leaves, just as on the mountain heights. Some of these small evergreen bushes, viz. the Crowberry and the common Ling (*Calluna vulgaris*), may be traced in an unbroken range from the plains up to a height of 2450 metres on the slopes of the Alps. Strange to say, these plants do not blossom much earlier on the lowlands than on the high Alpine regions, and it has actually been shown that *Calluna* blooms rather sooner at a height of 2000 metres than in the northern portion of the Baltic lowlands. How is this? The winter snow has long disappeared from the lowlands, while the hill-sides above are still concealed under their cold white covering. The winter snow has gone, to be sure, but not the winter! While everything around is already in blossom, while the ear is already visible on the stalks of rye, the neighbouring moor is still dismal, waste, and lifeless. A month or so later there is a stir on the dry soil of the cold moor, and the absorbent roots of the plants which have evergreen rolled leaves commence their activity. When the warm days of midsummer arrive and the sun sends down its powerful rays, the temperature of the soil quickly increases, and indeed rises far more than would be thought possible. The damp cushion of bog-moss at mid-day feels quite warm; and a thermometer placed 3 cms. below the surface in the uppermost mossy layer of a moor on a cloudless summer day (22nd June) showed a temperature of 31° C. while the temperature of the air in the shade was 13°! An unpleasant vapour rises from the damp earth, which settles on the surface, and makes a walk over the moor particularly disagreeable. Scarcely has the sun set in glowing red on the horizon when this vapour condenses into patches of mist which settle over the dark expanse; stems, branches, and leaves are covered with drops of water, and next morning everything is as thoroughly soaked as if it had rained throughout the night. This process, which is regularly repeated during the fine weather, is only interrupted when a damp wind from the sea blows, driving masses of cloud over the heath, or when copious rain saturates the soil. It needs no further showing that under such conditions an abundant and continuous transpiration from plants is impossible, and that in the short intervals which are allowed to the leaves for transpiration, the outlets from the wide-meshed spongy parenchyma must not be obstructed; and it does not need further proof that the evergreen rolled leaf is the form most suited and adapted to these conditions.

The flora of the Cape of Good Hope may not unjustly be compared with that of the Baltic lowlands—countless low bushes which are very like Heaths, Wild Rosemary, and Crowberry in appearance—all with small rigid evergreen leaves, and entire rolled-back margins; the upper side of the leaf usually dark green, the under side having the same arrangements as shown in the rolled leaves of plants growing on

moors which border the Baltic Sea, and in the cold Arctic tundra. This shrubby evergreen vegetation of the Cape belongs indeed in part to the same families as these. Heaths especially are to be found in abundant variety; as many as 400 species can be counted—many more than are furnished by the whole of the rest of the world taken together. But a great number of species from other families, viz. Rhamnææ, Proteaceæ, Epacridææ, and Santalaceæ, possess an exactly similar foliage, and without blossom and fruit are often indistinguishable from the heaths. This low evergreen bush vegetation is not distributed all over the Cape, but is restricted to the neighbourhood of the coast, to the country which slopes in terraces down to the south-west, and to the celebrated Table Mountain, rising abruptly above Cape Town. The aqueous vapour brought by the sea-winds condenses directly over these regions, and for five months, from May till the beginning of October, the soil is not only soaked by abundant rain, but what is perhaps of even greater moment, all the evergreen bushes are kept in a damp condition by the falling mist, and often are dripping with water just like the heaths on the moors of the Baltic lowlands. When the development of vegetation on the lower terraces of the south-west coast is at a standstill on account of the increasing dryness, the summit of the Table Mountain is still enveloped in the celebrated mass of cloud known as the "table-cloth", and the plants growing on the ridges and plateaus are during this time as much saturated as the Trailing Azalea, which robs the south wind of its moisture on the mountain ridges of the Central Alps. It is, however, in this damp period that the growth of the plants in question takes place. Most of the plants on the heights of the Table Mountain blossom and put forth new shoots in February, March, and April; on the lower terraces from May to September. In the northern regions and on mountain heights the beginning and end of the year's work in plants is limited by the cold, but in the Cape the dryness of the soil is the cause which brings the upward current of the sap in vegetation to a standstill for so long a time. At the coast, however, this dryness is never so severe that the plants are exposed to the danger of withering up altogether, as on the steppes.

As on the south-west coasts of the Cape, so is it round about the Mediterranean Sea and in the west of Europe, which is swept by sea-winds laden with vapour from the Atlantic; for example, Portugal and the south-west of France, which are in like case, characterized by an abundance of low bushes, with evergreen rolled leaves, and especially by some gregarious heaths. Here also the year's growth takes place in the wettest season, and arrangements must be made that during this period the formation of organic materials, the withdrawal of food-salts from the soil, and consequently unhindered transpiration may be carried on. Here, too, dryness interrupts the activity of the absorbent roots, and the evergreen vegetation of the coast-line extends inland as far as the damp sea-winds make themselves felt; while still further inland a steppe-like vegetation preponderates. The analogy presented by the Mediterranean flora goes so far that, on the southern point of Istria, for example, which may be compared as to shape with the south point of Africa, quantities of the evergreen *Erica arborea* are only to be found on the south-west

coast district on a comparatively narrow strip of land; while in the interior of Istria the waste dry terraces of the Tschitscherboden (which might be compared with the arid plains of the Cape) show no trace of a heath vegetation.

Why the plants with evergreen leaves which grow in the far north, on the heights of the Alps, on the Baltic lowlands, on the shores of the Atlantic Ocean, on the borders of the Mediterranean basin, and at the Cape of Good Hope are not all of the same species, is a question which cannot be answered here; yet it seems proper to point out that all plants furnished with evergreen rolled leaves, whose year's work is stopped by dryness, would freeze in countries where the earth in winter is covered with snow, i.e. the molecular structure of their protoplasm would be entirely altered by the frost, which would kill it; while the protoplasm of the analogous northern forms would suffer no harm from the cold. It is well worthy of remark in this connection that some of the last-mentioned plants have an extraordinarily wide distribution; that they may actually be found, quite similar in appearance, in the bleak north, and in the southern districts, if only those conditions of moisture which we have shown to account for the form of the leaves obtain in the places mentioned. Thus the Irish Heath (*Daboecia polifolia*) may be found along the Atlantic coast as far as Portugal, and the common Ling (*Calluna vulgaris*) grows just as well at a height of 2450 metres above the sea beside the glaciers of the Etzthal in the Central Alps, as further south on the Abazzia, surrounded by laurel groves on the sea-coast of Istria.

---

### 3. PREVENTION OF EXCESSIVE TRANSPiration.

Protective arrangements on the Epidermis.—Form and Position of Transpiring Leaves and Branches.

#### PROTECTIVE ARRANGEMENTS ON THE EPIDERMIS.

The relation of the form of the evergreen rolled leaf to transpiration is anything but exhausted in the foregoing account. The part played by this form of leaf, in particular during the dry season of the year, yet remains to be discussed. If it is necessary during the wet period that transpiration should be increased as much as possible, and that everything which might restrict the exhalation of aqueous vapour from the stomata should be kept away, it is also of importance that on the appearance of the dry season the equilibrium between the water taken from the soil and the water excreted by the leaves should not be destroyed, and that an excessive evaporation from the portions of the plant above ground should be hindered. New seasons bring new problems to be solved. At the time when the water-current begins to ascend from the soil saturated by the winter rains, we have an aid to transpiration; later on, in the dry period, we have a protection against the dangers which might attend excessive evaporation. It is certainly of great interest to see

how a whole group of the arrangements discussed above, among which the rolled leaf is not the least noticeable, serve, at different seasons of the year, and often at different times of the same day, two distinct purposes, as indicated.

First, the stomata themselves. While the green tissue has need of food-salts from the soil for the manufacture of organic materials, they cannot be too widely opened; everything is welcome, then, which promotes transpiration, and consequently assists in the elevation of fluid nourishment from the saturated soil. But if the temperature and dryness of the air increase after the green parenchyma has finished its yearly task, or if the soil from which the absorbent roots have hitherto derived their supply of fluid become so dry that the water exhaled from the aërial positions can no longer be replaced, it is of the greatest importance that the stomata should be closed. This is brought about by the two cells bounding the stoma, which have been termed the "guard" cells.

In order to clearly understand the mechanism of the opening and closing of stomata, it is necessary to examine the structure of these guard-cells more in detail. Both are bean-shaped in outline, their concave surfaces being turned towards the stoma; they are only connected with one another at their extremities. By their convex sides they are in contact with ordinary epidermal cells; their outer walls are in contact with the atmospheric air, and their inner walls with the spongy parenchyma. Both the innermost and outermost walls of the guard-cell are strongly thickened, but the wall by which they are connected with neighbouring epidermal cells, as well as that portion which directly borders the stoma, is relatively thin, elastic, and extensible. If the figure of two such guard-cells be imitated in caoutchouc, and they be fitted together like an actual closed stoma—water being forced into them under considerable pressure—the curvature of the thin and elastic portions of the walls will be most altered. The side wall in contact with the neighbouring epidermal cell bulges out, and at the same time the whole cell becomes elongated in a direction perpendicular to the surface. By this means the two guard-cells are forced apart. When the water is allowed to flow out of the swollen caoutchouc cells, they again fall back into position, the two portions of the walls which border the stoma coming into contact with each other and closing the opening. The same thing occurs in the actual guard-cells of the living plant. As soon as they become distended, they separate from one another; when they relax and resume their original position, they come closely into contact again. This process bears a strong resemblance to the changes in the cells of the pulvini at the base of the sensitive leaves of *Mimosa*, which will be described later, and it is highly probable that it may be traced back to a similar stimulation. That the guard-cells actually separate from one another by swelling up, i.e. by absorbing fluid, and then close together again in consequence of the loss of water, can be shown by first supplying water and then withdrawing it by a solution of sugar. In the former case the stomata open, in the latter they close, and it may therefore be considered an established fact that a closing movement is brought about by the extra loss of water in dry air. But if these pores, through which water vapour escapes when the plants

are full of sap, close as soon as there is a danger of too much evaporation, the mechanism must be considered as excellently regulating transpiration, and as providing a true preventative against over-evaporation.

This closure of the exhalent chambers in the interior of the leaf, important as it is, would alone be sufficient in but a very few cases to ward off this threatened danger. If the epidermis which stretches over the thin-walled transpiring cells of the spongy parenchyma is itself thin-walled and succulent, water will be exhaled from it also into the dry atmosphere; this loss of water from the epidermal cells is compensated for by water drawn from the neighbouring parenchymatous cells in the interior of the leaf, and ultimately the leaves would wither up if the supply of water from the roots were stopped or became insufficient. Therefore the epidermal cells must be adequately prevented from exhaling. When this is the case, and when the stomata are closed, the spongy parenchyma, and, generally speaking, all the succulent cells in the interior, are securely protected.

The walls of the epidermal cells in the first stages of their development are composed mainly of cellulose, and are uniformly thin and delicate on all sides. The outer wall, which is in contact with the air, then becomes thickened and divided into an inner and an outer layer. The inner retains its original character, but the outer—the so-called "cuticle"—undergoes great modifications. The cellulose becomes changed, and is replaced by a mixture of stearin and the glyceride of a fatty acid (suberic acid), forming a tallow-like fat which is termed *cutin* or *suberin*. In consequence of this metamorphosis the cell-wall becomes less and less permeable to water, and when it has attained a considerable thickness it becomes at length almost entirely impervious to water and aqueous vapour. Frequently, between the inner cellulose and the outer corky layer, other so-called "cuticularized layers" are formed, whose chief constituent is again suberin, and which often attain to a considerable bulk.

Aquatic plants, which are not exposed to the danger of excessive evaporation, of course do not require this protection. Plants whose leaves are surrounded by air, on the other hand, can never entirely dispense with it. The thickness of these corky layers is extremely variable according to the condition of humidity of the air. Where the air is very damp throughout the year, the outer wall of the epidermal leaf-cells appears to be only slightly thicker than the inner, and the cuticle only forms a thin continuous layer. On the other hand, plants which are temporarily exposed to dry air possess very highly developed cuticular strata. Especially when the leaves are evergreen and remain several years on the branches, as, for example, in the Holly (*Ilex Aquifolium*, see fig. 73<sup>2</sup>), and in the Oleander (*Nerium Oleander*, fig. 73<sup>3</sup>), the cuticular layers are so strongly developed that the outer wall of the epidermal cells is many times thicker than the inner wall. Evergreen parasites, as, for example, the Mistletoe (fig. 73<sup>1</sup>), those tropical orchids and Bromeliaceæ which live epiphytically on the bark of trees and are often exposed to great dryness in the hot season of the year, cactiform plants, and generally the majority of succulent plants, possess epidermal cells with very strongly thickened outer walls. This is so

also in the case of the pines with evergreen needle-shaped leaves, where, as a rule, the water compensating for that exhaled by the leaves cannot come quickly through open channels, but only slowly through the woody cells. Usually the cuticle and cuticular layers are of equal thickness over the whole leaf surface; this is so especially in smooth, shiny, leathery evergreen leaves. Not infrequently, however, an irregular thickening is seen, particularly in the neighbourhood of stomata, where circular ramparts are raised, as in *Protea mellifera* (see fig. 67<sup>3</sup>), or peg-shaped projections are formed, as in the Bamboo (see fig. 66), or elongated hair-like filaments arise, as in the rolled leaves of *Azalea* and many Heaths (see figs. 71 and 72).

It would, however, be erroneous to suppose that this formation of a thick cuticle on the epidermis is a peculiarity of evergreen leaves. Plants which are surrounded

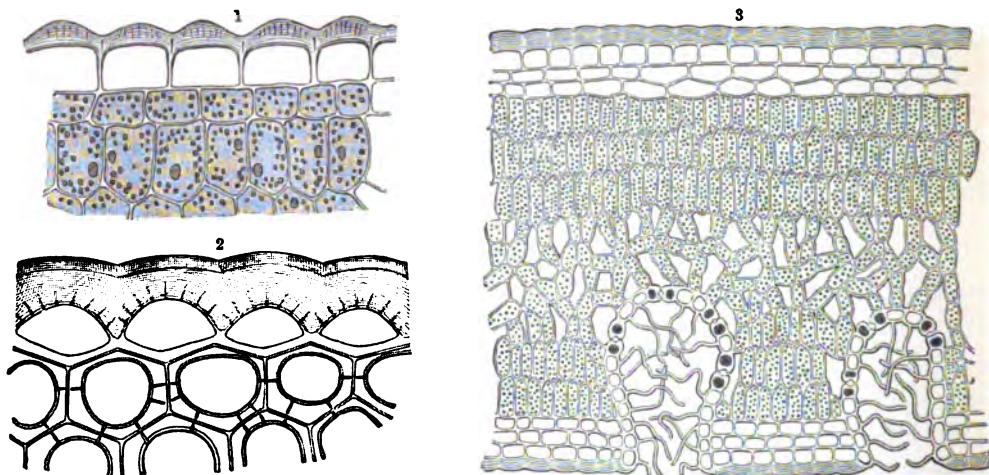


Fig. 73.—Thickened Stratified Cuticle.

<sup>1</sup> Vertical section of a portion of the leaf of Mistletoe (*Viscum album*);  $\times 420$ . <sup>2</sup> Vertical section of a portion of the leaf of Holly (*Ilex Aquifolium*);  $\times 500$ . <sup>3</sup> Vertical section of leaf of Oleander (*Nerium Oleander*);  $\times 320$ .

all the year by a damp atmosphere, and are never exposed in their natural condition to the danger of too much evaporation, very often have evergreen leaves, and yet the outer wall of the epidermal cells is not at all, or only very slightly, thicker than the inner; and conversely, plants with apparently thin delicate leaves, which are green only in the summer, have quite conspicuous thickening-layers. A knowledge of these conditions is of the utmost importance in plant culture, and gardeners know very well that many plants, although they appear to be capable of resistance, can never be removed from the damp air of the greenhouses, because the leaves then become desiccated like those of aquatic plants which have been taken out of water and exposed to the air. A species of palm, *Caryota propinqua*, which is represented in its native habitat in fig. 74 opposite, was grown in the botanical gardens at Vienna, and it developed in the damp air a magnificent stem with fine large leaves. On a summer day, when the temperature of the open air coincided with that of the greenhouse, this *Caryota*, together with the tub in which it was rooted, was carried into the open and placed in a somewhat shady place, but partly exposed



Fig. 74.—*Caryota propinqua*.

to the sun's heat. One day, after a warm dry east wind had swept for only a short time over the foliage, it became quite brown, and in the evening all the leaves were entirely dried up and dead. And yet leaf-segments of this palm appear to be firm, leathery, and dry, and one would have supposed them to be particularly well protected against drying up. The section of part of a leaf which is represented in fig. 75, however, corrects this impression. This shows that the epidermal cells are certainly very compact, by which the firmness of the leaf is materially increased, but that their walls are not thickened, being only like those of a delicate fern in this respect. Under these small thin-walled epidermal cells lie large succulent cells which form the so-called aqueous tissue, the structure of whose walls likewise cannot limit evaporation; below these are the large succulent cells of the green tissue. A glance at this leaf section will make it clear that this palm is well

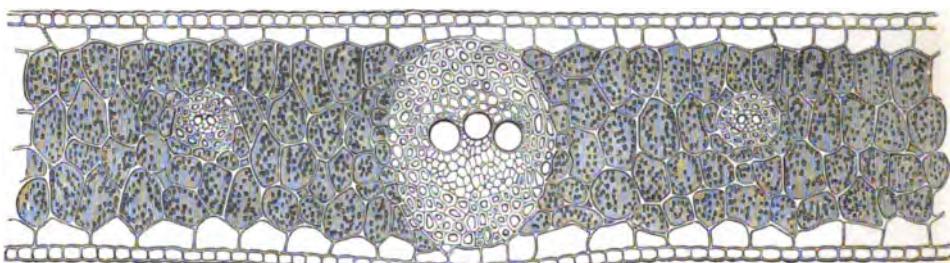


Fig. 75.—Vertical section of a portion of the leaf of *Caryota propinqua*;  $\times 200$ .

adapted to its warm damp habitat, where it is never exposed to a strong evaporation, but not to the dry, even if warm, air of a Continental climate.

To the wax-like excretions of the cell-wall which form a delicate bloom, easily rubbed off, on both sides of the leaf, frequently colouring it pale blue, grey, or white instead of dark green, it has already been stated that the rôle is assigned of protecting the stomata from moisture. From what has been said, one would expect that these waxy coverings, which are especially to be met with in the Cruciferae and Rutaceæ of steppes, in many acacias and Myrtaceæ of Australia, and in the pinks and spurges of the Mediterranean flora, would also be able to limit transpiration in the epidermis—that is, in the structures over which the bloom-like covering extends. Experiments specially undertaken, have also shown that in the same space of time, and under otherwise similar conditions, leaves whose bloom had been carefully rubbed off lost almost a third more water than others whose waxy covering had been left intact.

That the varnish-like covering of the epidermis, composed of a mixture of mucilage and resin ("balsam"), which is excreted from capitate hairs and other glandular structures, is able to restrict transpiration has also been pointed out. These coverings are especially developed in many plants of the Mediterranean flora, particularly in a whole group of *Cistus* (*C. laurifolius*, *populifolius*, *Clusii*, *ladaniferus*, *monspeliensis*, &c.); further in shrubby plants which develop late, in the height of summer—as, for example, in *Inula viscosa*, which is so abundant on the

coast. Plants of steppes and prairies (e.g. *Centaurea Balsamita* of the Persian steppes and *Grindelia squarrosa* in the prairies of North America) are likewise protected throughout life from over-vaporization by varnish-like coverings of this kind; while the foliage of Cherry, Apricot, and Peach trees, as well as of Birches, Sweet Willows, Balsam and Pyramidal Poplars, and the Black Alder, is only covered with such a varnish while young, when it has just burst from the buds, and the outer walls of the epidermal cells have not yet become sufficiently thickened; later on, however, when the cuticularized layers have become fully formed, this covering which limits transpiration disappears. Only on those places of the epidermis, where the outer walls of the cells remain very thin and permeable by fluids and gases, is this coat of balsam retained until the leaf is to be thrown off; but in this case it probably regulates the absorption of atmospheric water.

How far the *incrusterations of lime* and *salt excretions* take part in the absorption of atmospheric water by organs situated above the ground has likewise already been considered in the section on water absorption. It is obvious that these concretions and coverings of the epidermis must be capable of restricting transpiration. Incrustations of lime are principally found in plants which grow in the clefts and crevices of rocks; excretions of salt are only observed in shore-plants and those of steppes and wastes, but then always on low bushes and shrubs with small narrow leaves, and herbs whose foliage rests on the soil. The reason for this is again easily found. High trees could not support the weight of leaves loaded with incrusterations of lime and salt, even if their trunks and branches possessed the greatest strength imaginable.

It has been observed that plants whose leaves are covered by incrusterations of lime and salt, or whose epidermal cells are strongly thickened on their outer walls by corky layers, are almost always destitute of hairs; while plants, on the other hand, whose epidermal cells possess delicate outer walls, if they are not surrounded by a damp atmosphere throughout the year, nor submerged in water, are usually furnished with structures known as plant-hairs (*trichomes*); from which it may be inferred that the hairy covering of the leaf or stalk in question is able to protect it from drying up in just the same way as the corky layers. Of course only those hairs are meant whose protoplasmic contents have disappeared, and which have become sapless and filled with air; for those hair-structures, which consist of cells rich in sap and osmotic contents, would not help in preventing evaporation from the deeper tissue; they are themselves in need of protection, and special protective arrangements exist for them, as already set forth in the discussion on the absorption of water by aerial portions of the plant. Such structures would, if unprotected, give off water to the surrounding air, and continually absorb fluid from adjacent cells below them. This action does not take place in air-containing cells, and if their dry membranes, and the air which they inclose, are interpolated between the dry atmosphere and the succulent tissue below, this latter will be protected from evaporation, like damp earth covered with a layer of dry straw or reeds, or the fluid at the bottom of a bottle whose neck is closed with a plug of cotton-wool.

The importance of air-containing cells as a covering for succulent tissue must also be considered in another relation. It is well known that evaporation from the surface of fluid or a damp body is much increased by the warmth of the sun's rays. On the other hand, if the heating is restricted, so also is the evaporation. If we use a dry cloth to shade from the sun, we lower not only the temperature, but also the amount of evaporation from the shaded body. The covering of air-containing hairs on leaves may be compared to such dry screens, and its action may be demonstrated by the following experiment:—Take two of the bi-coloured leaves of a Bramble bush, which are smooth on the upper side, but covered with a white felt-work of hairs on the lower, and which are exactly similar in size and position with regard to the sun, being situated very near each other on the stem. If these leaves are wrapped round thermometers, in such a way that the leaf which covers one thermometer bulb has its white felted side turned towards the sun, that covering the other, the green hairless side, it will be found that the temperature in the leaf whose smooth green side is directed towards the sun will in less than five minutes rise 2°–5° above that of the leaf whose white felted side is so directed. If such leaves are plucked and exposed to the sun, some with the white felted side, others with the smooth green side uppermost, the latter always shrivel and dry up much sooner than the former. There can be no doubt, after this, that a dry coat of hair over succulent plant tissue, which is exposed to the sun's rays, considerably restricts the heating of, and exhalation from this tissue.

The significance of the coverings of hair on portions of plants turned away from the sun, particularly on the under sides of flat and rolled leaves, has already been discussed. These coverings are only of slight importance as a means of protection against over-transpiration. In rare cases, indeed, it happens that the hairy covering on the side of the leaf turned from the sun, the lining of the leaf, so to speak, must act as a protection, since the flat leaf-lamina is so twisted and turned that the sun's rays strike not on the upper but on the under surface. There are certain ferns of Southern Europe (*Ceterach officinarum*, *Cheilanthes odora*, *Notochlaena Marantæ*), which, contrary to the habits of most of this shade-loving group, grow on blocks and walls which are exposed to the burning sun. In these ferns the upper surface of the leaf is smooth, but the under, on the other hand, is thickly covered with dry hair-scales. In wet weather the leaves are spread out flat, with the smooth surface uppermost; in dry weather they become rolled up, and the under cottony side is then exposed to the sun and to dry winds. Among the low herbaceous growths of the Mediterranean flora, a like behaviour is shown by the widely distributed Hawkweed, *Hieracium Pilosella*, whose radical leaves, forming a rosette on the soil, appear green on the upper and white on the under side, by reason of a felt-work of star-shaped hairs. In places where the ground easily dries up, and when there have been no showers for a long while, it is usually seen that first the margins of the leaves turn up, and then by degrees the whole leaf becomes bent and rolled, so that the lower side is turned towards the sun's rays, and the white felt of hairs functions as a protective screen to the whole leaf.

The relations between the hairy covering on the upper side of the leaf and transpiration stand out, most strikingly, in those districts where plants during their vegetation period are, as a rule, exposed to dry air only for a few hours each day, and where their activity is not interrupted by a long warm dry period, but by frost and cold—as is the case, for example, in the Alpine region of mountain heights. On the Alps, the drying up of flowering plants by the sun only occurs in a very few



Fig. 76.—Edelweiss (*Gnaphalium Leontopodium*).

cases, viz., where the scanty soil on the narrow ledges of steep projecting rocks, and crags, and on rocky slopes, &c., is only watered by rain, mist, and dew. If no showers fall for several successive days, and the south wind blows over the heights with a clear sky day and night, these scanty layers of soil may dry up to such an extent that they are unable to supply the necessary fluid food to the plants rooted in them. Under these circumstances plants growing there have most pressing need of means of lessening transpiration in the leaves. In places such as these are to be found, almost without exception, plants whose leaves and stems are thickly covered on all sides with hairs, together with succulent plants and saxifrages incrusted with lime. This is the habitat of the felted Whitlow-grass (*Draba*

*tomentosa, stellata*), of the grey-leaved Ragwort (*Senecio incanus* and *Carniolicus*), of the magnificent silky Cinquefoil (*Potentilla nitida*), and of the white-leaved bitter Milfoil (*Achillea Clavennae*); especially is this the habitat of the most celebrated Alpine plants, of the scented Edelraut and the beautiful Edelweiss—the former (*Artemisia Mutellina*) with a grey shimmering silky coat, the latter (*Gnaphalium Leontopodium*) wrapped in dull white flannel. On looking at the vertical section of the Edelweiss leaf (see fig. 77<sup>1</sup>), one sees that the epidermal cells with their thin outer walls would be unable to regulate exhalation and drying in the sun, and that a powerful protection is afforded against too rapid evaporation, in case of extraordinary dryness, by the possession of a layer of sapless, air-filled, interwoven hair-structures. The Edelraut, Ragwort, and the other plants named, which grow on the sunny rocks of the Alps, show these same characters of leaf structure, and what has just been said about the Edelweiss applies fully to them also. It should be mentioned that on the heights of the Pyrenees, Abruzzi, and Carpathians, as well as on the Caucasus and Himalayas, the plants growing on sunny ridges of rock, where they are exposed to the wind, are covered with silk and wool exactly after the model of the Edelraut and Edelweiss, and that there is on the Himalayas an Edelweiss which is wonderfully similar to that of the European Alps. In the far north, on the other hand, where the flora in other respects has so much in common with that of the Alps, these plants are absent, and generally a search over the rocky crags for herbs and shrubs, whose leaves are furnished with silky or felt-like coverings on the upper surface, is futile. The genera which grow on these places and form a characteristic feature of the vegetation in consequence of their great abundance—as, for example, *Diapensia Lapponica*, *Andromeda hypnoides*, *Mertensia maritima*, *Draba alpina*, and others, possess remarkably smooth green leaves. When hairy coverings are present, they are restricted to the under leaf-surface, especially to that of rolled leaves. They are never found on the plants of rocky slopes, but only on those of damp marshy ground, or by the side of water which is for a short time free from ice. Here, however, they certainly do not help to lessen transpiration, but function in the way described above in the discussion on rolled leaves. It is indeed not too much to connect these facts with the conditions of the climate, and especially to explain the absence of plants whose foliage is silky or felt-like on the upper surface, by saying that a drying up of the soil and a limiting of the water supply never occurs on the narrow terraces of steep rocky declivities in Arctic regions, and that therefore there is no danger of over-evaporation to plants growing in those regions.

It is in keeping with this explanation that on Central and South European mountains, on whose heights an Alpine vegetation is to be found, the number of forms having silky and felted foliage increases as these mountains are situated further south, and the more they are exposed to temporary dryness. Plants of the Edelweiss type are still wholly foreign to the Riesen-Gebirge; in the Northern Alps their number is comparatively small, in the Southern Alps they increase in a surprising manner, and the summits of the Magellastock, the ridges of

the Sierra Nevada, and the mountains of Greece are unusually rich in such forms.

If plants growing in such situations are protected against the dangers of too rapid and too abundant evaporation, how much more must this be the case in those regions where, with the increasing warmth of summer, the number of showers steadily diminishes; and where the soil becomes dried more and more deeply, so that all the plants whose roots are near the surface are unable to derive a drop more water from it? All plants which are to survive the dry period in such places must during this time entirely cease transpiring—they must, as it were, turn into a chrysalis and sleep during the summer. They actually do this in all sorts of different ways, and by the most diverse means. One of the commonest and most widely spread methods is, without doubt, by having the transpiring organs clothed with a thick covering of dry air-containing hairs. Plenty of examples of this are furnished by the flora of the Cape, Australia, Mexico, the savannahs and prairies of the New World, and the steppes and deserts of the Old. In the dry elevated plains of Brazil, Quito, and Mexico, there are large tracts covered with gregarious spurge-like growths and grey-haired species of Croton, and when the wind blows, moving these bushes to and fro, undulations are set up over wide extents of country, the whole appearing like a billowy sea of grey foliage. A similar picture is presented by the *Painciras* belonging to the Compositæ, or by the *Lychnophora*, on the high plains of Minas Geraes in Brazil. Nowhere in the whole world, however, does the presence of hairs on foliage, as a protection against exhalation, appear in such an abundant and varied manner as in the floral region surrounding the Mediterranean, known as the Mediterranean district. The trees have foliage with grey hairs; the low undergrowth of sage and various other bushes and semi-shrubs (for which the name "Phrygian undergrowth", used by Theophrastus, may be retained), as well as the perennial shrubs and herbs growing on sunny hills and mountain slopes, are grey or white, and the preponderance of plants coloured thus to restrict evaporation has a noticeable influence on the character of the landscape. He who has only heard from books of the evergreen plants of the Greek, Spanish, and Italian floras, feels at the first sight of this grey vegetation that he has been in some degree deceived, and is tempted to alter the expression "evergreen" into "ever grey". Every conceivable sort of hair structure is to be met with in these parts—coarse felt-work, thick velvet, and white wool mixed in endless variety. Here is a leaf looking as if covered with a cobweb; there another as if bestrewn with ashes or clay; here a leaf surface, covered with closely pressed hairs or scutiform scales, glistens like a piece of satin; and here again is a plant with such a long flock of hair that one might imagine that sheep in passing had left pieces of their fleece hanging on it. There is hardly a family in the flora of the Mediterranean district which does not possess members richly provided in this way. The Composites are the most remarkable in this respect, especially the genera *Andryala*, *Artemisia*, *Evax*, *Filago*, *Inula*, and *Santolina*; then come the Labiates of the genera *Phlomis*, *Salvia*, *Teucrium*, *Marrubium*, *Stachys*, *Sideritis*, and *Lavandula*; rock-roses, bindweeds, scabious,

plantains, papilionaceous plants, and plants of the Spurge-laurel family—just those plants which constitute the main part of the vegetation on the shores of the Mediterranean Sea, and which possess a thickly-woven covering of hair. Indeed representatives of families such as the Grasses, whose members are usually bare, here appear to be quite shaggy with hair. It is also very interesting to see that so many species, which have a wide range of distribution, and which, from Scandinavia to the coasts of the Mediterranean, have bare foliage, can in the South protect themselves from drying up, by developing hairs on their epidermis. For instance, from Northern and Central Europe as far as the Alps, the epidermis of the stems and foliage of *Silene inflata*, *Campanula Speculum*, *Galium rotundifolium*, and *Mentha Pulegium* is smooth and bare; in the South,—particularly in Calabria,—the leaves and stems of these species are covered with thick down.

Next to the Mediterranean flora, the neighbouring Egyptian and Arabian desert regions, the elevated steppes of Persia and Kurdistan, as well as the lowlands of Southern Russia and the plains of Hungary, show a comparatively large number of species whose leaves are thickly coated with hairs on both surfaces. Their number is less than that of the flora of the Mediterranean district, because in the steppes and deserts the dryness of the summer is greater than in that region, and even thick hairy coverings are not always a sufficient protection against this dryness, and also because in some of these districts the dry period passes directly into a severe winter, and the hairs would offer but a poor protection against the cold. Since on the coasts of the Mediterranean Sea the winter temperature never falls below freezing point, evergreen and grey leaves remain there unmolested, and recommence their activity at the beginning of the next season.

The successive developments of certain plant forms are very instructive with regard to the relations existing between whole floral regions and transpiration. In the steppes, Mediterranean district, and at the Cape, bulbous plants and annuals first make their appearance; then follow the perennial grasses and woody plants; and finally succulent plants and thickly-haired immortelles. The numerous tulips, narcissi, crocuses, stars of Bethlehem, asphodels, amaryllises, and all the other bulbous growths, which begin to sprout immediately after the first winter or spring rain, always have bare foliage. Their transpiration is very active in consequence of the rapidly-increasing temperature of the air, but the saturated soil provides a sufficient substitute for the evaporating water, and also has ready in a free state the food-salts which are required for rapid growth. The shrubs which sprout at the same time, the peonies and hellebores, as well as the host of annuals which spring up, blossom, and fructify in an inconceivably short time, almost all possess bare foliage, especially in the steppes. Towards midsummer, when the drought commences, all these plants are already in fruit; their foliage, which until now has been actively at work, begins to turn yellow and to dry up; their succulent tubers and bulbs are imbedded below the surface in soil which is now as hard as a stone; and the seeds which have fallen from the annual plants are easily able to survive the aridity of the summer and the severity of the winter, since they are inclosed in

protective coverings of great variety. Any plants which are still to retain their activity during the summer on the steppes or in the Mediterranean floral district would succeed very badly if only furnished with the bare foliage of the spring vegetation. If such a plant is to be protected from drying up, its transpiration must be lessened. This is effected by various protective arrangements, but best of all by a thick coating of hair. The papilionaceous plants and species of Orache, above all the immortelles and wormwoods (*Helichrysum*, *Xeranthemum*, *Artemisia*), which are still in bloom in the height of the summer and can bear the strongest heat of the sun, are, as a rule, thickly covered with hair, and regions, which perhaps only a month before were clothed in fresh green, are now shrouded in dismal gray. With the transition from the wet period of the spring and winter rains to the dryness of midsummer, there is a corresponding gradual transition from the green of the bare, succulent hyacinth leaf to the grey of the rigid felt-covered leaf of the immortelle.

A peculiar appearance is shown in Mediterranean floral districts by many biennial and perennial plants which one spring give rise to a rosette of leaves close to the soil, and in the spring following to a stem bearing both leaves and blossom, which arises from the centre of the rosette. This rosette formed in the first spring has to live through the dry hot summer, and is therefore covered with felted grey hairs; the stem formed in the second year which gives rise to the blossom, since it is formed during the wet period, has no need of the protective hairs, and is therefore furnished with green foliage. The *Salvia lavandulifolia* and *Scabiosa pulsatilloides* of Granada, the *Hieracium gymnocephalum* of Dalmatia, and in the Mediterranean flora the wide-spread *Helianthemum Tuberaria* may be mentioned as examples of such plants. Their appearance is so strange that one involuntarily asks whether this green leafy stem really belongs to the grey rosette of leaves, or whether some one has not been playing a joke by putting together the stem and rosette of two different kinds of plants.

These hair-like structures, called "covering hairs", whose function is a protection against excessive exhalation, exhibit a very great variety with regard to form. Notwithstanding this diversity, however, a certain degree of uniformity must not be overlooked, inasmuch as in individual species the same kind of hairs are always present. The coat of hair contributes not a little to the characteristic appearance of the species, and therefore has always been considered of especial value in description and discrimination. As a help to description the older botanists introduced a series of expressions into botanical terminology by which to denote shortly and tersely the most pronounced varieties, and this seems to be the most suitable place for explaining these terms—*i.e.*, the forms of covering hairs which are signified by them.

First, those covering hairs consisting of a single epidermal cell, which grows out beyond the other epidermal cells, must be distinguished and set apart from those which have become multicellular by the formation of separation walls.

*Unicellular* clothing hairs in many cases only project slightly above the surface

of the leaf to which they belong; they bend down nearly at a right angle almost immediately above their place of insertion, so that the long tapering part of the hair cell lies on the leaf-surface, as shown in fig. 77<sup>3</sup>. When such hair-forms, in great numbers and parallel to one another, entirely cover the surface of the leaf, light is strongly reflected from them, and the surface looks just like a piece of silk. Such a covering of hair, which is seen particularly well on the shining foliage of the South European bindweeds (*Convolvulus Cneorum*, *nitidus*, *oleæfolius*, *tenuissimus*, &c.), is termed "silky" (*sericeus*). Two varieties of this may be distinguished, viz. the more usual case in which all the hairs of the leaf lie parallel with the midrib, and the rarer case where the hairs assume a different position on the right and left of the midrib, the whole of those on either side being respectively parallel to the lateral ribs of their respective sides. The reflected light then only meets the eye of the observer, in any one position, from one half of the leaf, the other half therefore appearing dull. In such a case the whole leaf has that peculiar shimmer, changing on the slightest movement, which we admire on the wings of certain butterflies, and which is also shown by that variety of silken material known as satin. When the unicellular hairs do not lie on the surface, but rise up from it, the shimmer is altogether absent, or is only present to a small extent. If the hairs are short, very numerous, and closely pressed together, they are said to be "velvety" (*holosericeus*); if they are of greater length and situated further apart, the expression "shaggy" (*villosum*) is used. Hairs which consist of single elongated air-containing cells, much twisted and bent, with thin and pliant walls, are called wool-hairs, and the covering formed by them is said to be "woolly" or "tomentose" (*lanuginosus*). Woolly hairs are always twisted spirally, sometimes loosely, sometimes tightly—frequently almost like a corkscrew. As a rule the spiral is in the opposite direction to the movement of the hand of a watch, whose direction is said to be to the left. It should also be noticed whether the elongated twisted cells of the wool-hairs are circular in cross section, as in the South European *Centaurea Ragusina* (see fig. 77<sup>5</sup>), or whether they are compressed like a ribbon, as in *Gnaphalium tomentosum* (fig. 77<sup>4</sup>). The latter case is by far the most common.

*Multicellular* clothing hairs originate by the repeated division of certain epidermal cells caused by the formation of separation walls. These dividing walls are either all parallel to the surface of the leaf or stem, or some of them are perpendicular to the plane of the leaf. In the first case the cells are usually arranged like the links of a chain, and are termed jointed or articulated hairs. When such articulated hairs are short and not interwoven—as, for example, is the case in the beautiful gloxinias (see fig. 77<sup>2</sup>), the surfaces clothed with them appear like velvet; when they are elongated, curved, and twisted and entwined, the leaf appears to be covered with wool (see fig. 77<sup>1</sup>), and to the naked eye this form of covering is the same as that already stated to be shown by unicellular covering hairs. Silky coats are also produced by multicellular hairs, even by such a peculiar form as is represented in fig. 78<sup>3</sup>. These hairs are developed in the following manner. A superficial cell by the formation of a septum parallel to the leaf-surface divides into two

daughter-cells; the division is repeated and gives rise to a small chain of three, four, or five short cells which project slightly above the surface of the leaf. The top cell does not divide further, but enlarges in a striking manner, not, oddly enough, lengthening in an upward direction, but transversely, parallel to the leaf-surface, forming a lancet-shaped, rod-like structure, which shades the leaf, and is supported by its sister cells as if on a pedestal. Thousands of such curious hair-structures,

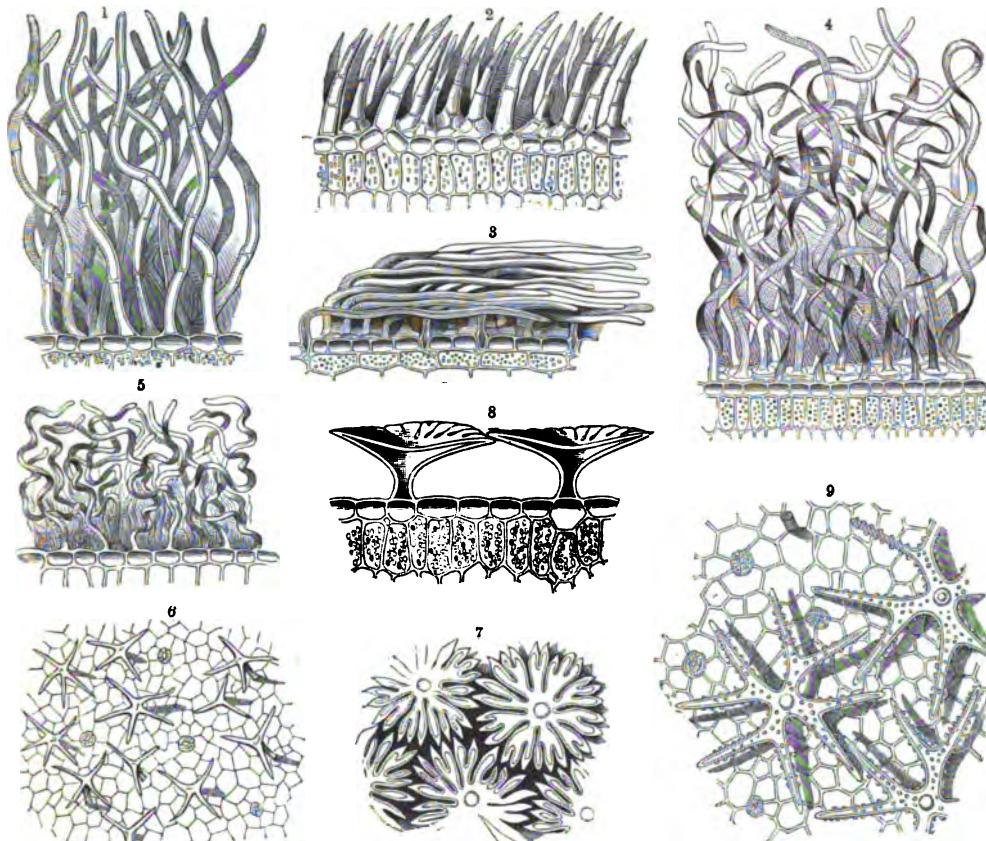


Fig. 77.—Covering Hairs.

<sup>1</sup> Articulated woolly hairs of *Gnaphalium Leontopodium*. <sup>2</sup> Articulated velvety hairs of *Gloxinia speciosa*. <sup>3</sup> Silky hairs of *Convolvulus Cneorum*. <sup>4</sup> Ribbon-like flattened woolly hairs of *Gnaphalium tomentosum*. <sup>5</sup> Spiral woolly hairs of *Centaurea Ragusina*. <sup>6</sup> Stellate hairs of *Alyssum Wierzbickii*. <sup>7</sup> Umbrella-shaped hairs of *Koniga spinosa*; surface view. <sup>8</sup> Vertical section of the same hairs. <sup>9</sup> Stellate hairs of *Draba Thomasii*.  $\times$  about 50.

which may best be compared to compass-needles, clothe the surface of the leaf in close proximity to each other, and when they are arranged in a regular manner, they reflect the light uniformly, and produce a distinctly silky lustre. If they are twisted, this lustre is lessened to a greater or less extent. This variety of hairs, called T-shaped, is distributed in a remarkable way. Numerous species of *Astragalus*, the scabious of the Mediterranean flora (*Scabiosa cretica*, *hymelita*, *graminifolia*), several Crucifers (*Syrenia*, *Erysimum*), native on the steppes of Southern Russia, the magnificent *Aster argophyllus* of Australia, and particularly numerous

species of wormwoods; the South European *Artemisia arborescens* and *argentea*, the *Artemisia sericea* and *laciniata* belonging to the steppes and Siberian flora, the Common Wormwood, *Artemisia Absynthium*, and the frequently-mentioned Edelraut, *Artemisia Mutellina*, growing on the rocky crags of mountain heights—all owe their silky appearance to these T-shaped hair-structures.

It may also happen that the cell which is elongated transversely (*i.e.* parallel to

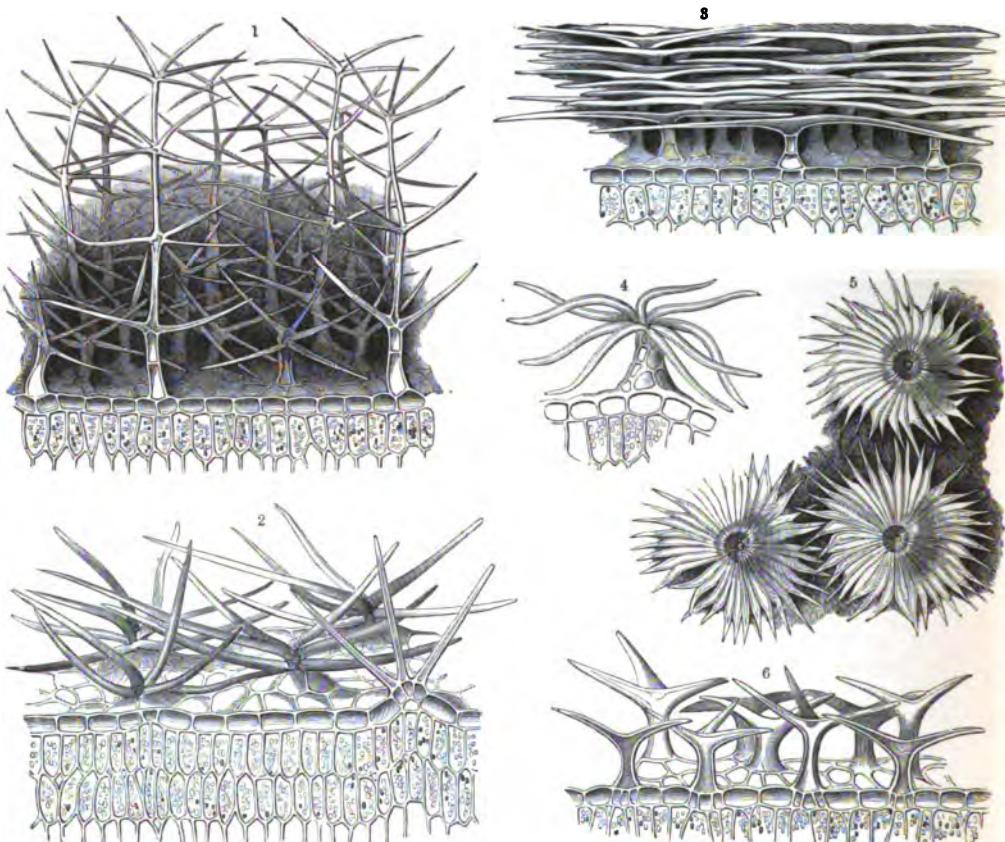


Fig. 78.—Covering Hairs.

<sup>1</sup> Floccose hairs of *Verbascum thapsiforme*. <sup>2</sup> Tufted hairs of *Potentilla cinerea*. <sup>3</sup> T-shaped hairs of *Artemisia mutellina*. <sup>4</sup> Actinia-like hairs of *Correa speciosa*. <sup>5</sup> Scutiform scales of *Elaeagnus angustifolia*. <sup>6</sup> Stellate hairs of *Aubretia deltoidea*.  $\times$  about 50.

the leaf-surface), and which is the uppermost of the small group of cells projecting above the epidermis, is prolonged in three, four, or even more directions, so as to have a stellate appearance. Thus the covering of the leaf is seen to consist of three, four, or many-rayed stars, each supported on a short stalk (see figs. 78<sup>6</sup> and 77<sup>6</sup>). The rays of the stellate cells are frequently forked, as in *Draba Thomasii* (see figs. 77<sup>9</sup>). In rare cases they have a comparatively large central portion, and are only divided at their circumference into short rays; they then look exactly like small sunshades spread out over the leaf-surface. This elegant form, which is represented in figs. 77<sup>7</sup> and 77<sup>8</sup>, has a particularly beautiful appearance in

*Koniga spinosa*, a member of the Mediterranean flora. All these clothing hairs, with star-shaped indented upper cells, are grouped together under the name of "stellate hairs" (*pili stellati*). In Cruciferæ and Malvaceæ they occur in endless variety.

When the uppermost cell of the group forming the stellate hair is divided by separation walls, which in part are placed perpendicularly to the leaf-surface, branched hairs are the result. In branched hairs the branches, which are almost

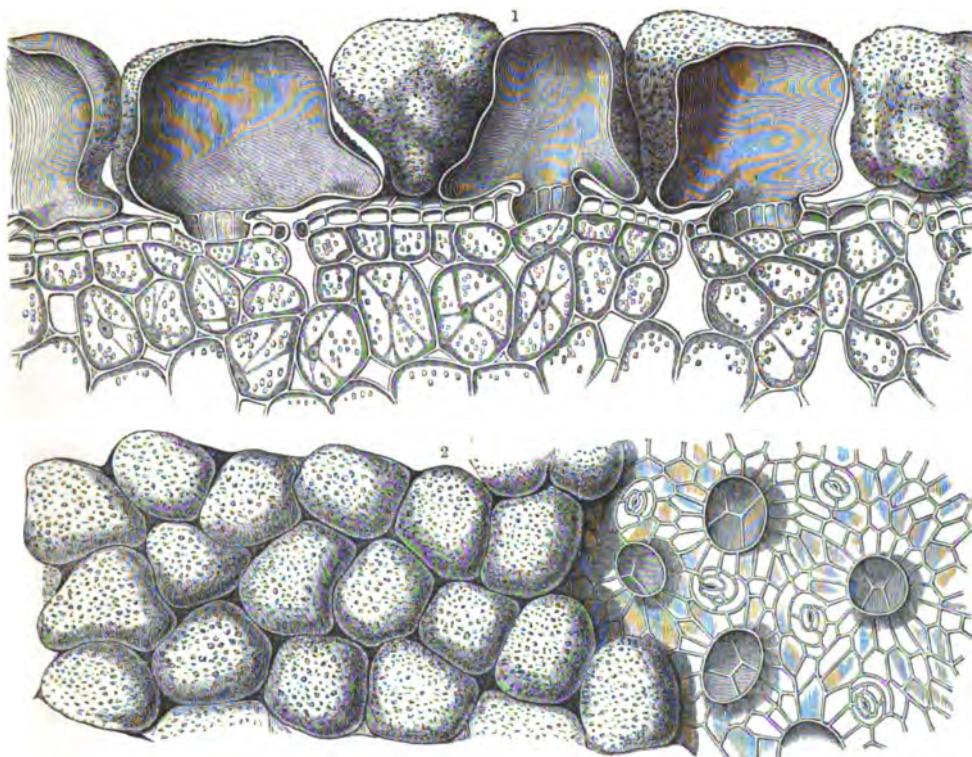


Fig. 79.—Flinty armour of *Rochea falcata*.

<sup>1</sup> Section perpendicular to the leaf-surface. <sup>2</sup> Surface view; on the right hand the vesicular distended portion of some superficial cells is removed and the stomata are brought into view;  $\times 250$ .

always arranged in a stellate manner and are usually unicellular, can be distinguished from the part which supports the branches. This portion usually looks like a pedestal, and is sometimes multicellular, sometimes formed from a single cell. When the pedestal is very short, and the cell supported by it is divided by several radiating divergent septa, which are either oblique or perpendicular to the leaf-surface, tufted hairs (*pili fasciculati*) are formed. These look like sea-urchins lying on the surface in close proximity to each other; they vary very much in the size, number, length, and direction of their branches, and they are particularly abundant on the cinquefoils (*Potentilla cinerea* and *arenaria*), cistus and rock-roses (*Cistus* and *Helianthemum*). A common form is represented in fig. 78<sup>2</sup>. When the foot-stalk is very short, and the radiating branch-cells borne by it are

joined to one another, a star-shaped, ribbed, multicellular plate, indented at the margin, is produced (see fig. 78<sup>6</sup>). These plates are generally flat, lie level on the surface of the leaf or stem, overlap one another with their indented margins, and cover the green surface of the leaf so completely that it appears to be white instead of green, and invest it with a bright, almost metallic, lustre. Such leaves are said to be "scaly" (*lepidotus*). The best known examples of such leaves, covered with shining silvery hair-scales, are those of *Elaeagnus* and of the Sea Buckthorns (*Hippophaë*). If the plates are bent, irregularly fringed, and lustreless, the leaf covered with them looks just as if it were strewn with bits of clay, and is said to be "clayey" (*furfuraceus*). Examples of this are well shown by the leaf-coverings of many plants allied to the Pine-apple (Bromeliaceæ). When the top cell of the hair is supported on a moderately high pedestal, and is divided into numerous radiating daughter-cells which diverge from one another, a structure is produced which is somewhat like a knout, or, if the radiating cells are short, like a sea-anemone (*Actinia*). This form of hair is seen, for example, in the Southern and Eastern European *Phlomis*, in many mulleins (*Verbascum Olympicum*), and, with multicellular pedicels, on the leaves of *Correa speciosa*, an Australian shrub (see fig. 78<sup>4</sup>). Occasionally a branched hair produces several whorls of branches above one another, and then hair-structures are formed which resemble stoneworts (Characeæ) or miniature fir-trees under the microscope. When many such tiny tree-like hairs are placed close together with interwoven branches, they look under a magnifying-glass like a small plantation, and the analogy is heightened if one-storied tree-shaped hairs, like the undergrowth in a high forest, occur under the higher many-storied ones. This is the case in the Torchweed, *Verbascum thapsiforme*, whose hairs are represented in fig. 78<sup>1</sup>. Hair-structures like these appear to the naked eye like flock, and are described as "floccose" hairs (*pili floccosi*). Many of these have the peculiar habit of rolling themselves together into small balls, which make the leaf-surface look as if it were bestrewn with coarse white powder. This is the case, for example, in the mullein known as *Verbascum verulatum*.

In the crowded condition of stellate and tufted hairs, of branched floccose and unbranched woolly hairs, it is unavoidable that the neighbouring hair-cells should cross one another, intertwine, and be more or less interwoven; and thus arises a felted mass which covers the surface of the organ in question. Such hair-masses are termed "felt" (*tomentum*), and the varieties are distinguished as "felted" (or "tomentose") stellate or woolly hairs, &c. Often the felt only forms a thin loose layer, through which the green of the leaf-surface can be seen; but occasionally it is so thick that the leaf appears snow-white.

While in all these cases the covering which protects the leaves and stem of the plant from over-transpiration is woven from air-containing cells, cylindrical and elongated—usually, indeed, very much elongated—in some thick-leaved plants, especially in species of the genus *Rochea*, a native of the Cape, these cells become vesicular and distended; they are arranged in rank and file adjoining one

another, so that taken together they form a layer which spreads over the other epidermal cells like a coat of mail. The ordinary epidermal cells are small and only slightly thickened on their outer walls, as shown in the illustration above. The cells which are placed together to form the armour, however, are enlarged in quite an unusual way; their stalk-like base, looking as if wedged in between the ordinary epidermal cells, is indeed comparatively large, but the bladder-like swollen portion exhibits dimensions which are about six hundred times greater than those of the ordinary epidermal cells. The vesicles are closely packed together, and become almost cubical by the mutual pressure they exert on each other. Where a space might occur, the bladders form protuberances and bulgings at the side which fit in together in such a way that a completely closed coat of mail is the result. The expression "coat of mail" is the more justified here since the swollen bladder-like cells of *Rochea* are as hard as pebbles. Large quantities of silica are present in the cell-walls, and by burning them a complete skeleton in silica can be obtained, as in the case of the silica-coated Diatomaceæ. It needs no further explanation that in the dry season such a coat of armour affords to the succulent cells it covers an excellent protection against evaporation.

There is, however, still another point to be considered. The vesicular swollen cells on fully-grown leaves are still occupied by protoplasm, which forms a thin layer round the walls, while in the centre is a large cavity filled with cell-sap; it is only in older leaves that the bladder-like cells become filled with air. As long as they contain watery cell-sap they serve as reservoirs of water from which the green chlorophyll-bearing cells below can obtain supplies at the periods of greatest drought, when all other sources are exhausted. This fact, that the water-reservoirs are situated on the exterior of the plants, where there exist so many aids to exhalation, shows how well the silicified walls of these bladders function. They may be compared to glass vessels whose mouths are directed towards the green tissue, and whose walls allow absolutely no water to pass through.

#### FORM AND POSITION OF THE TRANSPIRING LEAVES AND BRANCHES.

The enlargement of the green leaf-surface has been already explained as a means of increasing transpiration, which is of special importance when the plants considered grow in damp air. Similarly a diminution of the green surface signifies a restriction of transpiration. This relation is illustrated by the fact that in all floral areas, in which the activity of the vegetation is restricted or entirely stopped by increasing dryness, the foliage of the plants is not so widely outspread, i.e. it undergoes a diminution. It is also a well-known fact that one and the same species, if grown in a dry sunny position, will exhibit smaller, and in particular, narrower leaves than when it has been grown in a damp situation. This is well seen in passing from the mountainous districts bordering the Hungarian lowlands to the plains of the lower regions. A number of shrubs and herbs, *Anchusa officinalis*, *Linum hirsutum*, *Alyssum montanum*, *Thymus Mareschallianus*, &c., exhibit on

the dry sands of the plains much narrower leaves than in the valleys of the mountainous regions. In conjunction with the narrowing of the foliage, the wrinkling of the leaves has to be considered, *i.e.* the formation of grooved depressions on the surface. Strictly speaking, there is no lessening of the whole surface of the leaf, but only of that portion of the surface which is exposed to sun and wind. This is the point with which we are concerned. With regard to the exhalation of water, only the extent of the surface directly influenced by the agents for increasing transpiration is to be considered; whilst the extent of the grooved depressions, which are not exposed to the sun's rays, nor to dry currents of air, may be in a certain measure neglected. On the whole, plants with wrinkled and grooved foliage are not very abundant. For the most part the crumpling is to be seen on quite young leaves when first they break through the bud-scales, and when their epidermal cells are not yet sufficiently thickened with cuticular material. Later, when the formation of the cuticle is advanced, the wrinkles gradually become smooth, and the leaf becomes flat.

It has already been pointed out that those pit-like depressions, on the floor of which stomata are concealed (cf. figs. 68 and 73), may also serve to restrict transpiration. There is no contradiction in the statement that the same structure at one time hinders the entrance of water and the wetting of the stomata at the bottom of the pit, and at another time prevents direct contact with dry winds and consequent over-transpiration. Each has its turn. When the foliage of the Australian Proteaceæ, during the summer sleep, is exposed for months to the scorching rays of the sun and to the warm dry air, and when all supplies of water from the soil have ceased, evaporation from the leaves must be restricted as much as possible; it is then that the pit-like depressions perform their duty in this respect. When, later on, the plants are aroused from their long sleep, and have to provide themselves with food, to grow, blossom, and fructify in an extremely short space of time, while violent showers of rain are pouring down from the clouded sky, and all the leaves are dripping with wet; it is then very important that, in spite of these exceedingly unfavourable conditions for evaporation, an abundant transpiration should nevertheless take place, and that the function of the stomata should be in no way impaired by the moisture. These pit-like depressions, which in the dry period prevented evaporation, now have to keep moisture away from the stomata.

In many plants evaporation from the superficial tissue is restricted by the close contact of the leaves to their supports, like the scales on the back of a fish. The upper side of a leaf in contact with the stem, and frequently adhering to it, is thus deprived of the means of exhalation, and transpiration can only take place on the somewhat arched or keeled under side of the green scale-like leaf. This occurs, for example, in the Tree of Life (*Arbor vitæ*), in several species of Juniper, in *Thujopsis*, *Libocedrus*, and various other Conifers. It is not without interest to notice that in several of these Conifers the little green scale-like leaves only become close pressed to the stem when they are exposed to the sun, whilst they project from it if the branches in question are shaded.

A further reduction of the evaporating surface is brought about by the development of thickened or fleshy leaves. In order to render the points under consideration as clear as possible, it is perhaps well to insert here the following observations. By altering the form of a sheet of lead 8 cms. square and 1 mm. thick into a solid cylinder, the diameter of this cylinder is seen to be only 1 cm., and the whole surface of the cylinder is only one-fifth of that of the previous flat sheet. The application of these figures to the tissue of a leaf demonstrates how much smaller is the transpiring surface of a thick cylindrical leaf than of a thin flattened one. Such thickened leaves, which approach more or less to the cylindrical shape, are to be found regularly where transpiration has to be reduced for a considerable time—as, for example, in the mountainous districts of Central and Southern Europe, in the genus *Sedum*, growing on sandy soil which easily dries up, and on stone walls and battlements (*Sedum album*, *reflexum*, *dasyphyllum*, *atratum*, *Bolonicense*, *Hispanicum*, &c.). They also occur in a striking manner in many tropical orchids which grow on rocks, or epiphytically on the bark of trees in the East Indies, Mexico, and Brazil, exposed for more than six months to great aridity (*Brasavola cordata* and *tuberculata*, *Dendrobium juncum*, *Leptotes bicolor*, *Oncidium Cavendishianum* and *longifolium*, *Sarcanthus rostratus*, *Vanda teres*, and many others); but especially are they found in aloes and stapelias and species of *Cotyledon*, *Crassula*, and *Mesembryanthemum*, whose habitat is in the driest districts of the Cape. Several Umbelliferæ, Compositæ, and Portulacæ (*Inula crithmoides*, *Crithmum maritimum*, *Talinum fruticosum*) growing on stony places of the sea-shore in the burning sun, and many salsolas of the deserts and salt steppes, as well as finally some Proteaceæ, which for two-thirds of the year are exposed to the droughts of Australia—all are characterized by their development of fleshy leaves.

Just as thick-leaved plants have acquired their succulence by a modification of their foliage, similarly, in the so-called cactiform plants, it is the stems which become thick and fleshy, and take on the functions of leaves. Here the green tissue is situated in the cortex of the stem, the epidermis covering it contains stomata just like the epidermis of foliage-leaves, and the green cortex transpires, and functions on the whole exactly as the green leaves do. When the stems of the cactiform plants are richly branched and the branches are short, they sometimes much resemble thick-leaved plants. Frequently also the separate portions of the stem and branches take the form of fleshy leaf-like discs, as in the genus of the Prickly-pear (*Opuntia*), and such stem-structures are usually mistaken by the uninitiated for thick leaves. Gardeners, as a rule, group the thick-leaved and cactiform plants together under the single term "succulent plants". To the cactiform plants belong the opuntias and cacti, species of *Cereus*, *Echinocactus*, *Melocactus*, and *Mamillaria*, which are distributed from Chili and South Brazil over Peru, Columbia, the Antilles, and Guatemala. These are, however, especially developed on the high plains of Mexico in astonishing variety of form. To the cactiform plants belong also the leafless candelabra-like tree-shaped spurges

of Africa and the East Indies. These plants are exposed, far more than the thick-leaved plants, for the greater portion of the year to extraordinary dryness. Their usual habitats are dry sandy and stony plains, waste rocky plateaus, and crevices of rocks which are almost completely wanting in soil. They always inhabit regions where no rain falls for about three-fourths of the year, and which usually belong to the driest parts of the earth. The whole organization of these plants corresponds to these conditions of their habitat. Dry scales and hairs are produced instead of foliage-leaves, or these are often metamorphosed into thorns which project in great numbers from the thick stem-structures, and efficiently protect them from the attacks of thirsty animals. The epidermis of the pillar-like, disc-shaped, or spherical stem-portions is thickened on the outer wall, so as to almost resemble cartilage, and frequently it forms a coat of mail round the deeper-lying green tissue by the abundant deposition of oxalate of lime (as much as 85 per cent). Most of the succulent plants, whose cell-walls, which are in contact with the air, are fortified by oxalate of lime, silicic acid, or suberin, have in their tissue peculiar aggregates of cells which apparently serve for the storing-up of water for the dry season, and which have been termed "aqueous tissue". The water in these reservoirs is always so apportioned that it lasts from one rainy season to another; that is to say, the adjoining green tissue which exhales the stored-up water does not suffer from drought during the dry season. Also, it is contrived in these plants that, immediately after the fall of the first rain, the reservoirs are again filled with water, and that the emptying and filling of the cells and the decrease and increase of their volume exercise no harmful influence on the adjoining tissue. Succulent plants have been not inaptly compared to camels, the "ships of the desert", which provide themselves with a large quantity of water, and are then able to dispense with further supplies for a long time without injury. The cells of the aqueous tissue are comparatively large and their walls thin; the active protoplasm within forms a delicate layer round the walls—that is to say, a sac whose cavity is filled with watery, often somewhat mucilaginous, fluid. In the cactuses the aqueous tissue is hidden as much as possible in the interior of the thick rod-shaped or spherical stem; also in many thick-leaved plants, such as some of the European species of the genus *Sedum* (e.g. *Sedum album*, *dasyphyllum*, *glaucum*); in South African species of the genera *Aloë* and *Mesembryanthemum* (e.g. *Mesembryanthemum blandum*, *foliosum*, *sublacerum*), the aqueous tissue is concealed in the interior of the leaf, and is usually composed of cells surrounding vascular bundles there situated. In *Sedum Telephium*, known by the name of Orpine, as well as in species of House-leek (*Sempervivum*), and many salsolas growing on steppes, the ramifications of the vascular bundles are enveloped in a mantle of green tissue, and the bundles, which are, as it were, overlaid with green cells, are so arranged with regard to the colourless aqueous tissue, that to the naked eye they look like green strands in a transparent matrix which is as clear as water. In the Mexican Echeverias the aqueous tissue is inserted as broad stripes in the green tissue, and in the thick-leaved orchids it appears as if sprinkled between the green

cells. The epidermis in numerous other thick-leaved plants serves as a store-house for water in a marvellous way. Individual epidermal cells are then greatly enlarged and project beyond the others in the form of sacs, clubs, or bladders, as shown in the picture of *Rochea* (fig. 79). These bladders either fit together into a one-layered extended coat of armour, or they are frequently placed irregularly side by side or above one another. In some instances they form isolated groups or occur singly, and appear then to the naked eye like protuberances on the green stems and leaves, where they glitter and sparkle in the sunshine like an embroidery of dew-drops. Many leaves and branches—as, for example, those of the widely-distributed Ice-plant (*Mesembryanthemum cristallinum*)—have the greatest resemblance to candied fruit covered with clear, colourless, sparkling sugar crystals.

When the walls of the enormously-distended vesicular or bladder-shaped cells of the epidermis are silicified, as are those of the repeatedly-mentioned *Rochea*, it is easily understood that the watery cell-sap which they contain is not exhaled into the air; the fluid is, so to speak, inclosed in a glass bottle and can only be given off in the direction of the green tissue. But when the walls of the bladder-like giant cells are not silicified, and not even particularly thickened, what is the result? From the aspect of the Ice-plant one would think that a single warm dry day would suffice to shrivel and dry up the watery vesicles. But this is certainly not the case. Leafy twigs cut from the Ice-plant may be left all day on the dry ground in dry air and sunshine, and the large bladder-like cells on the surface will not lose their aqueous contents. After a week they become collapsed, having given up their water, not to the atmosphere, but to the green tissue covered by this swollen coat. Without doubt this phenomenon is to be associated with a peculiar formation of the cell-wall; but it is as certain that the constituents of the cell-sap, which fills the vesicles are also important, and it must be assumed that substances are dissolved in this aqueous fluid which restrict the evaporation of the water.

These substances, which hold water with great energy, and thereby enable the plants in question to survive through periods of the greatest dryness, are partly viscous, gummy, and resinous fluids, partly salts. It is well known that the sticky, watery pulp of crushed mistletoe berries, used in the manufacture of "bird-lime", may be exposed to the air for months without quite drying up, and the mucilaginous juices of many cactuses and thick-leaved plants behave in a similar manner, especially those of the Cape aloes, which exhale no water, and enable the plants possessing them to withstand the drought for months. In the thick-leaved plants of the salt steppes and deserts, the fluids are rarely resinous or gummy, but they frequently contain a surprising quantity of salts dissolved in water, such as common salt, chloride of magnesium, and the like; and these also obstinately retain water in proportionately large quantities. It is one of the most surprising of phenomena to see the thick-leaved salsolas rising above the soil of salt steppes, green and succulent, when the ground is at its driest in the height of summer, when for months no clouds have tempered the sun's rays and not a drop of rain has fallen, and when almost all other plants have long ago turned yellow and faded. The large amount

of salts contained in the sap of these plants renders them capable of a resistance which is almost greater than that afforded by mucilaginous materials and gum-resins.

It must, however, be remarked here that not all green leaf- or stem-cells containing abundant water have the function of storing it up for a dry season, and that the aqueous cell-groups and strands adjoining the green tissue, especially the so-called outer aqueous tissue, in very many cases, has another important function, viz. the conducting of carbonic acid to places where it can be assimilated, but this will be described in the next chapter.

An extreme reduction of the leaf-surface, combined with a formation of green transpiring tissue in the cortex of the stem, is also shown in another group of plants known by the name of "Switch" plants. They are characterized by thin rod-shaped stems and branches, while the cactiform plants, on the contrary, always have their axes but little branched, and massive, thickened, fleshy and rigid stem-structures which are unaffected by the wind. The switch-plants may be subdivided into those which are flexible, hollow, and only slightly branched—as, for example, the horse-tails (*Equisetum*), reeds (*Scirpus*), rushes (*Juncus*), bog-rushes (*Schoenus*), and several cyperuses (*Cyperus*); and into broom-like shrubs with rigid woody boughs breaking up into innumerable branches and twigs. The former are distributed over the whole world; the latter are principally to be found in Australia and in districts bordering on the Mediterranean Sea. In Australia it is chiefly Casuarinas and some genera of Papilionaceæ and Santalaceæ (*Sphaerolobium*, *Viminaria*, *Leptomeria*, *Exocarpus*) which take on this odd form, and some of them even attain to the size of trees. In the Mediterranean flora isolated species and groups from the families of Asparagineæ, Polygalaceæ, and Resedaceæ are seen with thin, stiff, rod-shaped, leafless branches, which project stiffly into the air with green cortex; but again, most of these plants belong to the Papilionaceæ and Santalaceæ. Several switch-plants of the papilionaceous genera *Retama*, *Genista*, *Cytisus*, and *Spartium*, growing together, often cover wide tracts of country in densely-crowded masses, and thus contribute not a little to the scenic peculiarity of the district. Many small rocky islands off the coast of Istria are entirely overgrown by *Spartium scoparium*, which is represented in the illustration opposite. In May large golden flowers, scented like acacias, appear on the green rods of the Broom, and then for a short time the dark green of the switch-plant is changed into a brilliant yellow. On passing near the coast, just at this time, the remarkable phenomenon is seen of golden yellow islands rising above the dark blue sea. This floral adornment is, however, but transitory, and nothing more monotonous and desolate than such a dry unwatered islet, covered with these shrubs, can be imagined.

The *Spartium* belongs to those switch-plants which are not entirely leafless, but which develop little green lancet-shaped leaves at intervals on their long twigs. But these are of such secondary importance that their green tissue can only form the smallest portion of the organic substances necessary to the further growth of the plants, and this duty chiefly falls to the share of the cortex of the switch-like branches. The cortex is also characteristically formed in accordance with this fact.

Under the epidermis, whose outer walls are much thickened and coated with wax, is the green transpiring tissue or "chlorenchyma", consisting of from five to seven rows of cells. This green tissue does not form a continuous mantle round the stem, but is divided into from ten to fifteen thick strands by strips of hard bast (see fig. 81). Below this cortex of alternating green tissue and strips of bast are soft bast, cambium, wood, and a very large pith; but these have no further interest for us here. It is, however, worthy of remark that in the green strands of the cortex



Fig. 80.—Swith-planta.

Bushes of *Spartium scoparium* near Rovigno in Istria.

of the *Spartium*, the crowded green chlorophyll-containing cells of the chlorenchyma closely adjoin one another, and that only very narrow air-passages ramify between them, so that here there is no formation of a spongy parenchyma penetrated by wide canals and passages. On the other hand, large cavities occur where the green tissue touches the epidermis, and these act as substitutes for the wide ramifying canals. Over each of the cavities a stoma is to be seen in the epidermis through which the water vapour, exhaled chiefly from the green cells, can escape (see fig. 81<sup>2</sup>). The stomata are proportionately small, but their number is very great. Since the guard-cells are not so strongly thickened on their outer walls as are the other epidermal cells, the stomata appear to be somewhat sunken. By this arrangement, and also by the epidermal coating of wax, they are protected from moisture.

In the Casuarinæ and in *Cytisus radiatus* (see fig. 69), the green tissue is distributed in the cortex of the branches exactly as in the case just described; but the strips of green tissue traversing the stem are deeply cut into by longitudinal furrows. In some other leafless switch-shrubs, such as species of the genus *Ephedra*, the chlorenchyma forms a continuous and uniform mantle round the stem, uninterrupted by strips of bast. But in this case the stomata are distributed uniformly over the whole surface of the rod-shaped branches, while in the brooms, Casuarinæ, and in *Cytisus radiatus* they are absent from those portions of the epidermis which cover the strips of hard bast.

Plants with leaf-like branches or cladodes are distinguished from switch-plants

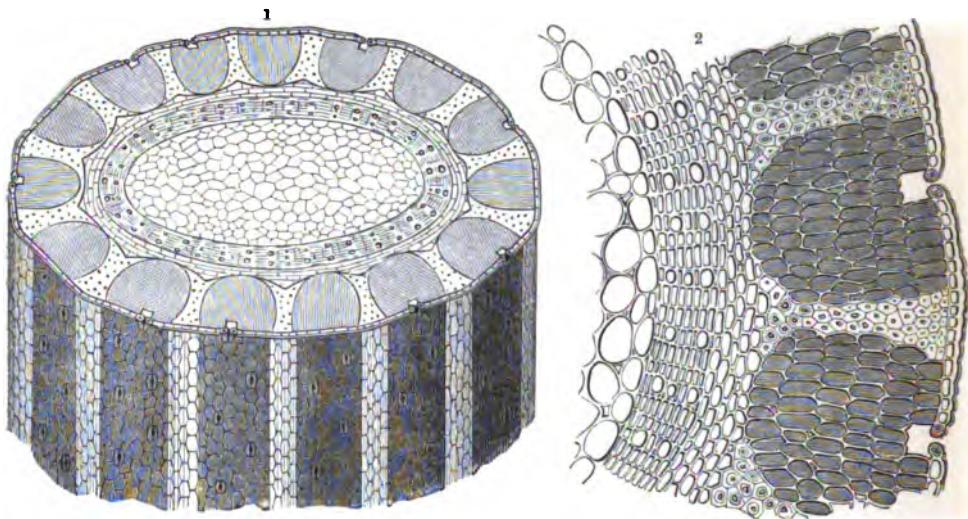


Fig. 81.—Switch-shrubs.

<sup>1</sup> Part of stem of *Spartium scoparium* cut transversely;  $\times 30$ . <sup>2</sup> Part of the transverse section;  $\times 240$ .

by the fact that all their shoots are not circular in section, but some are flattened, looking as though they had been pressed out. When this flattening is restricted to the so-called "short branches", i.e. when on a stem only the ultimate, comparatively short branches are flattened, the main axes remaining cylindrical, like ordinary stalks, these structures have quite the appearance of leaves which are sessile on the rounded stems. This explanation of them, however, given by botanists, is not at first sight satisfactory to the uninitiated. Why should these flat green structures be branches, and not leaves? The illustration opposite at once makes the matter clear. It represents two cladode-bearing plants, viz. two species of Butcher's-broom (*Ruscus Hypoglossum* and *aculeatus*), each at an early stage of development and also when fully grown. On the young shoots, which have just made their way out of the soil (see figs. 82<sup>1</sup> and 82<sup>2</sup>), the true leaves can be seen in the shape of small sessile pale scales on the long, rounded, finely-ridged axis; and from the angles which these scales make with the long axis arise darker, much thicker organs which rapidly increase in size, while the supporting covering-scales become dry, shrivel up, and finally

disappear, leaving no traces. Since the members which arise from the axes of leaves (whether these are small clothing-scales, or large green laminae does not matter) are not considered to be leaves, but shoots, the flat leaf-like structures of the Butcher's-broom are also regarded as shoots, and are named "flattened shoots" (cladodes)—or, considering their similarity to leaves, "leaf-branches" (phylloclades).



Fig. 82.—Plants with Leaf-like Branches (Cladodes).

<sup>1</sup> Young shoot of *Ruscus Hypoglossum*. <sup>2</sup> The same branch fully grown, with flowers on the cladodes. <sup>3</sup> Young shoot of *Ruscus aculeatus*. <sup>4</sup> The same branch with flowers on the cladodes.

This view is strengthened materially by the fact that these leaf-like structures, in their further development, and in the production of shoots, behave exactly like ordinary cylindrical axes. That is to say, small scale-like leaves spring from them, and from the axes of these scales arise stalked flowers (see figs. 82<sup>2</sup> and 82<sup>4</sup>) which ultimately fructify. Plants possessing such phylloclades are not very numerous on

the whole. The Butcher's-brooms, chosen above as examples, belong to Southern Europe, and occur in large quantities on the soil of dry woods, where everything is wrapped in deep sleep during the height of summer. In the Antilles, and in the prairies of the East Indies, are about twenty shrub-like species, belonging to the genus *Phyllanthus* of the Spurge-family. New Zealand also possesses one of these peculiar phyllocladous plants, belonging to the papilionaceous genus *Carmichaelia*. In the species of both these genera (see fig. 83) the flattened shoots are exceedingly like lancet-shaped foliage-leaves, and the true leaves are transformed into small pale scales. These tiny scales are situated on the margins of the phylloclades, and from their axils arise stalks bearing the flowers and fruit. On the Andes of South America occur the remarkable colletias, of which a species, *Colletia cruciata*, is represented in fig. 83. The leaflets on these extraordinary shrubs are diminutive, but not pale and scale-like; whilst the green phylloclades, which play the part of the foliage-leaves, form very strong flattened organs, tapering to a point, and placed opposite one another in pairs, so that each pair is always at right angles to the couple next above or below. Yet another arrangement is seen in *Coccoloba platyclada* (Polygonaceæ), a native of the Salomon Islands, and in *Cocculus Balfourii*, growing in the island of Socotra. But it is impossible here to enter into all these variations in detail; it is enough to have brought forward the most striking forms of phyllocladous plants which are represented in figs. 82 and 83.

If in all these peculiar plants the branches are flattened and spread out, it cannot indeed be asserted that the surface of their transpiring tissue has undergone diminution, and thus far of course this strange development has nothing to do with the restriction of transpiration. The arrangement by which this is brought about must be sought for elsewhere. It consists in this: the leaf-like shoots are so directed that their surfaces are vertical and not horizontal. Contrary to most flat leaves, which turn their broad surfaces fully to the incident light, the flattened shoots are placed vertically so that at mid-day they only cast a very narrow shadow, and do not stop the sunbeams on their way to the soil. It is obvious, however, that such a leaf-like structure placed vertically, as it were on edge, will exhale much less than a foliage-leaf whose surface is opposed to the mid-day sunbeams. The work carried on in the green cells, under the influence of light, is not hindered by this position of the leaf-like organs. If the vertical green surfaces are not so well illuminated by the sun's rays during the warmest part of the day, this is abundantly compensated for by the fact that their broad surfaces are exposed to the light both of the morning and evening sun. On the other hand, when the sun rises and sets, the heat is not so powerful, and consequently there is no such rapid exhalation to be feared as when the sun is in the zenith. To put the matter shortly, transpiration alone—not illumination—is restricted by the vertical position of the green laminae, and therefore this metamorphosis has rightly been considered a protective measure against excessive transpiration.

This arrangement is only found in plants of dry regions, where transpiration

requires no assistance, but where, on the contrary, the danger is often imminent that water cannot be drawn from the soil in sufficient quantity to replace that lost by exhalation.

The phylloclades, moreover, are only a type of a large number of organs which, in a word, all agree in this; the edge or narrow side of the flattened exhaling structure, not the broad surface, is turned towards the zenith. In many of the



Fig. 83.—Plants with Leaf-like Branches (Cladodes).

<sup>1</sup> *Colletia cruciata*. <sup>2</sup> *Carmichaelia australis*. <sup>3</sup> *Phyllanthus speciosus*.

vetches of the Southern European flora (*Lathyrus Nissolia*, *Ochrus*), but especially in a large number of Australian shrubs and trees, principally acacias (*Acacia longifolia*, *falcata*, *myrtifolia*, *armata*, *culturata*, *Melanoxyton*, *decipiens*, &c.), it is the leaf-stalks which are extended like leaves placed vertically, and then the development of the leaf-lamina is either entirely arrested, or has the appearance of an appendage at the apex of the flat green leaf-stalk, or "phyllode", as it is called. In many Myrtaceæ and Proteaceæ, especially in species of the genera *Eucalyptus*, *Leucaden-*

dron, *Melaleuca*, *Protea*, *Banksia*, and *Grevillea*, the leaf-blades themselves are not placed horizontally like those of our maples, elms, beeches, and oaks, but vertically on edge, like the phylloclades and phyllodes. Imagine now an entire wood of such eucalypti and acacias, on which the mid-day sun is pouring down its rays. If it is not exactly literally true to say that each vertical leaf only casts a linear shadow at noon, it is at least certain that there is not much shade on the ground of such a wood. The sunbeams find their way everywhere between the erect leaf-blades, penetrating the depths below, and it is impossible to speak of the dim forest-light under such circumstances. The Casuarines, which grow with eucalyptus, acacias, and Proteaceæ do not help to make such woods shady, and thus one is quite justified in speaking of the shadowless forests of Australia.

Although Australia stands alone in the variety and abundance of its plants possessing vertical leaf-blades, other floral areas furnish numerous and remarkable examples of this arrangement. One has only to think of the curious shape of the so-called "equitant" leaves belonging to many plants of the Daffodil family (*Tofieldia*, *Narthecium*), numerous irises, and the closely-related genera, *Gladiolus*, *Ferraria*, *Witsenia*, *Montbretia*, &c., chiefly natives of the Cape. The leaves exhibit the peculiarity of being folded together lengthwise, and the sides thus brought into contact become fused to one another. Only at the point where they join the stem do the two halves remain distinct, forming a groove in which is inserted the base of an upper leaf. The formation of such equitant leaves from ordinary leaf-blades may perhaps be illustrated by taking a strip of paper smeared on one side with paste and folding it longitudinally so that the pasted sides are in contact and become joined together. Such equitant leaves are so directed that their broad surfaces are much less exposed to the perpendicular rays of the mid-day than to those of the rising and setting sun.

In the Mediterranean flora, and on many steppes, plants are not seldom to be met with whose leaves look as if they had not been able to free themselves from the stem. In such plants the projecting portion of the foliage-leaf is very small, but the margins are continued for some way down the stem as projecting strips and wings. Leaves of this kind are termed "decurrent". They are particularly abundant amongst Composites, viz. in the genera *Centaurea*, *Inula*, *Helichrysum*; but they also occur in many Papilionaceous plants and Labiates. The position of these vertical wings, which traverse the stem, is exactly the same, with regard to the sun, as that of the phyllodes, phylloclades, and equitant leaves, and they behave in respect to transpiration in exactly the same way.

In many plants the blades of the foliage-leaves when young have not a vertical position, but gradually assume it during development, i.e. the blades at first are turned so that the flattened surfaces are horizontal and face upwards and downwards. Later they twist round at the point where they are inserted on the stem, so that their margins become directed upwards and downwards. As already stated, this peculiarity is observed in many eucalypti and various other Australian trees and shrubs. But plants in sunny situations in other regions also exhibit this

peculiarity. In the Spanish flora, for example, is an Umbellifer (*Bupleurum verticale*) whose leaves are so twisted with regard to the sun that they remind one forcibly of the Australian acacias. Many Composites, especially the widely-distributed Wild Lettuce (*Lactuca Scariola*), growing on dry soil in Central Europe,



Fig. 84.—Compass Plants.

<sup>1</sup> *Silphium laciniatum*, seen from the east. <sup>2</sup> The same plant seen from the south. <sup>3</sup> *Lactuca Scariola*, seen from the east. <sup>4</sup> The same plant from the south. Both species are considerably reduced.

exhibit this contrivance in a striking manner. A Composite shrub, *Silphium laciniatum*, to be found in the prairies of North America, from Michigan and Wisconsin as far south as Alabama and Texas, has obtained a certain renown by reason of the remarkable twisting of its leaf-blades. It long astonished hunters in the prairies that in these plants (represented in fig. 84) the leaf-laminæ, especially those springing from the lowest portions of the stem, not only assumed a vertical

position, but that the broad surfaces of each leaf always faced the rising and setting sun. Healthy living plants as they grow in the sunny meadows look as though they had been laid between two gigantic sheets of paper, somewhat pressed, and dried for some time in the way plants are prepared for herbariums, and had then been removed from the press and set up so that the apex and profile of the vertical leaf-blades point north and south, *i.e.* in the meridian; while their surfaces face the east and west. This inclination is so well and regularly observed by the living plants on the prairies, that hunters are enabled to guide themselves over such regions, even under a clouded sky, by means of these plants; for this reason *Silphium laciniatum* has been called a "compass" plant. The life of the compass plant is assisted by this placing of the vertical leaves in the meridian, in that the broad surfaces are placed almost at right angles to the incident sunbeams which illuminate them in the cool and relatively damp morning and evening, while at the same time they are not too strongly heated nor stimulated to excessive transpiration. At mid-day, on the other hand, when the sun's rays only fall on the profile of the leaves, the heating and transpiration are proportionately slight. It is of interest that the leaves of these compass plants, as well as those of the above-mentioned Lettuce represented with the compass plant in fig. 84, show this inclination and position when they grow on level, moderately dry, unshaded ground, and that in damp shady places, where there is no danger of over-transpiration from the powerful rays of the noon-tide sun, the twisting of the leaves does not take place, and they are not brought into the meridian.

The placing of their leaf-blades parallel to the ground when in the shade, but vertically when in dry sunny places, is, generally speaking, a phenomenon which may be seen in very many plants, including shrubs and trees. A species of lime, a native of Southern Europe, viz. the Silver Lime (*Tilia argentea*), is particularly noticeable in this respect. On dry hot summer days the leaves assume an almost vertical position, but only on those boughs and twigs which are exposed to the sun. If the tree stands at the foot of a wall of rock, or on the edge of a thick wood, so that a portion of it is shaded, the leaves on this shaded part remain extended horizontally. Such a tree then presents a strange aspect, as the leaves are of two colours—dark green on the upper side, and white on the under surface by reason of a fine felt-work of white stellate hairs—and it is scarcely credible at first sight that the shaded and sunny portions of the tree belong to one another.

In the compass plants and also in the Silver Lime the alterations in the direction of the leaves are brought about by alterations in the turgidity of certain groups of cells in the leaf-stalk. It is exactly the same cause which produces the periodic movements of numberless plants with pinnate or palmate leaves, and the leaf-folding of many grasses; and it is natural to conjecture that these phenomena of movement are also connected with transpiration. This is in part actually the case. In consequence of alterations in turgidity of the pulvini, the pinnate leaflets of the Gleditschias and some Mimosas rise up after sunset, while those of the Amorphas fall down, and assume a vertical position during the night; but this is con-

nected with the nocturnal radiation of heat (as will be explained later) and not with exhalation. It is, however, equally certain that the placing together and folding up of leaves and leaflets in many other plants is brought about in order to prevent over-transpiration and consequent withering up. Many shrubby, thorny mimosas of Brazil and Mexico, when in their native habitat and position, extend their leaflets horizontally when evening approaches, contrary to the behaviour of the well-known Sensitive Plant (*Mimosa pudica*), and they remain in this position throughout the night. Next morning they are still widely outspread. As soon as the sun has risen, and its beams fall on the foliage, the leaflets shut together; the menacing thorns, which until now have been hidden by the extended leaves, become apparent; and the leaflets remain in the vertical position during the hottest and driest hours of the day. Towards sunset they again rise and are extended horizontally. There is but one exception to this cycle of changes—if the opened leaf is shaken by the wind, and if the sky has been gray and clouded all day. In the former case, under the influence of the wind, a rapid closure occurs; in the latter case, when the weather is bad, they remain open all day. One of the Rutaceæ, *Porliera hygrometrica*, behaves like these mimosas. In Peru, the native country of these plants, where they abound, the opening and closing of the leaves has even been made use of for weather predictions, for when the vertical leaves are closed, dry hot weather can be reckoned upon; when they are open, damp cool weather. In the cultivated Bean (*Phaseolus*), moreover, alterations of position in parts of the leaflets may be observed to take place during the day. When the sun is powerful, the leaflets assume a vertical position, so that at noon the sun's rays only reach a small portion of the blade.

In several species of Wood-sorrel belonging to the South African flora, and also in the widely-distributed Common Wood-sorrel (*Oxalis Acetosella*), it may be noticed that the leaflets, as soon as they are directly struck by the sun's rays, sink down, so that their under surfaces—on which the stomata are situated—face one another, the three leaflets together forming a pyramid; while these same leaflets in damp shady places remain extended. The leaflets of the water fern, *Marsilea quadrifolia*, which grows in marshes and is distributed through Central and Southern Europe, temperate Asia, and North America, are very similar to those of the Wood-sorrel, but carry their stomata on the upper surface. As long as they remain floating on the surface of water, these leaflets are extended, but as soon as the water-level sinks and the leaflets become surrounded by air, they fold together above in the sunshine, and their position becomes vertical, precisely as in the compass plants.

As another phenomenon of this kind the periodic folding or closing of the leaves of grasses must be specially mentioned. It has long been noticed that certain grasses exhibit a very different aspect according as they are observed on a dewy morning or in the noon-day sunshine. In the morning their long linear leaves are fluted on the upper surface, or spread out quite flat. As soon as the humidity of the air diminishes, in consequence of the higher position of the sun, they fold

together lengthwise; again after sunset they widen and become flat or fluted. This process may be repeated twice on a summer's day within twenty-four hours, if a storm intervenes at mid-day and is followed by a sunny afternoon. How much this depends upon the conditions of humidity of the air, is demonstrated by the fact that such grasses, when grown in pots, can be easily made to open and close their leaves by alternately sprinkling them with water and placing in damp air, and then for a short time exposing them to dry air. The leaf-folding in various species of *Sesleria* is exceedingly quick and also very interesting. The species of this genus grow principally on the Alps, Carpathians, and Balkans. They always grow together and often cover wide stretches of hilly and elevated districts with thick grassy turf. One species (*Sesleria caerulea*) is distributed over Northern Europe in Finland, Sweden, and England. The closing of the leaves of these moor-grasses reminds one strongly of the Venus Fly-trap (*Dionaea muscipula*), which has already been fully described. It is indeed an actual shutting together of the two halves of the leaf. As in the leaf of the "Fly-trap", the midrib of the leaf of the *Sesleria* remains in its original position unaltered; also the two halves of the leaf do not come flatly in contact, but rise up obliquely so as to leave between them a deep, narrow, groove-like cavity, widest at its lowest part (see fig. 85<sup>2</sup>). While the open leaf turns its upper surface, rich in stomata, towards the sky, the two raised halves of the folded leaf are parallel with the incident sunbeams, and the folded leaf of the moor-grass may then be compared to the equitant leaf of an iris. In the cavity produced by the closing up of the leaf are the stomata, however, and thus the green tissue next them is excellently protected from the sun's rays as well as from the direct action of the wind. The epidermis of the lower surface, which is exposed on the folded leaf to all the agencies which excite transpiration, possesses no stomata, but is provided with a thick cuticle.

A leaf-folding similar to that of *Sesleria*, along the midrib, has been observed in the leaves of *Avena planiculmis*, which grows in sunny fields on the Sudetics and Carpathians. It also occurs in *Avena compressa*, and many others related to these species. The folding or closing of the leaves in the large section of fescue-grasses (*Festuca*) is carried on somewhat differently. In *Sesleria*, the opened upper surface of the leaf forms only a single shallow groove, and the folding only occurs at the midrib; but on the upper side of the fescue-grass leaf several parallel grooves are to be seen, and the green tissue is divided up by these grooves into several projecting ridges, exhibiting a very remarkable structure. In each ridge can be distinguished the base which forms a part of the under side of the whole leaf; then the apex opposite the base, belonging to the upper surface of the entire leaf; and finally, the two side portions forming the sloping sides of the grooves which run between the ridges (see figs. 87 and 88).

The greater part of each ridge consists of green tissue. The stomata on the ridge only open on the sloping sides facing the grooves. Neither the crests of the ridges nor the lower surface of the leaf exhibit a single stomate. The apex is without chlorophyll, and almost always has a border of elongated cells with strong elastic

walls under the epidermis; the same thing occurs on the under side of the leaf (*i.e.* at the base of the ridges), which is formed of one or several layers of cells without chlorophyll, but furnished with thickened walls. The closing of the leaf is not so simple here as in the *Seslerias*. There the leaf-folding only produced a single deep channel, widened at its base; in the fescue-grasses all the small grooves between the ridges become narrowed by the closing, *i.e.* by the upward inclination of the right and left halves of the leaf, those adjoining the central ridge to the greatest

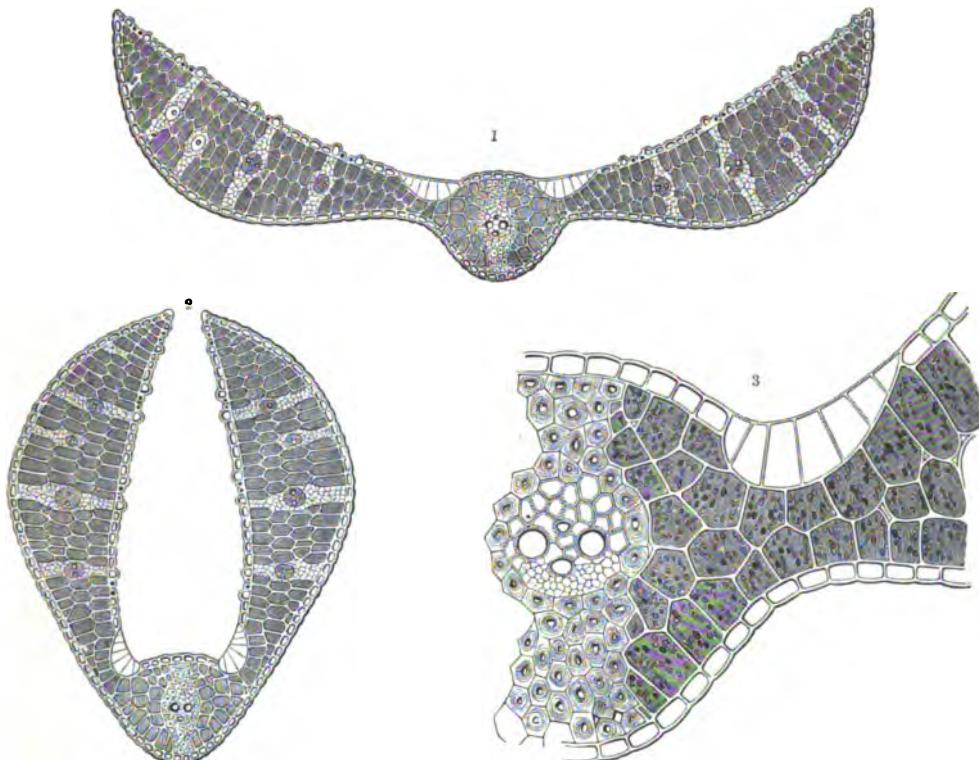


Fig. 85.—Folding of Grass-leaves.

<sup>1</sup> Vertical section through an open leaf of the thin-leaved Moor-grass (*Sesleria tenuifolia*). <sup>2</sup> Vertical section through a closed leaf;  $\times 40$ . <sup>3</sup> Portion from the centre of an open leaf;  $\times 800$ .

extent, those in the neighbourhood of the approximated margins in a lesser degree (see fig. 88<sup>2</sup>). Since the stomata lie on the sides of the ridges, it is obvious that transpiration is checked to the utmost by the closing and consequent approximation of the opposite sides of each groove.

In individual cases among various fescue-grasses are to be found manifold differences in the number and shape of the ridges, also with respect to the formation of the under surface of the leaf, and most of all in the form assumed by the leaf in its expanded condition. There is a large group of festucas which are said to be poisonous by the shepherds in the mountain regions of Spain, and in the Alps, the Taurus, and the Elbruz. These will be spoken of again later. When open in damp weather they form only a moderately narrow main furrow, with several

narrow secondary grooves leading from it, as can be seen in a vertical section of an open leaf of *Festuca alpestris*, a plant very abundant in the Southern Alps (see fig. 86<sup>5</sup>). In *Festuca alpestris*, the blunt apex of each ridge has a border, three layers deep, of cells destitute of chlorophyll, and the lower side of the leaf is provided with an actual armour of thick-walled bast cells, covered by an epidermis.

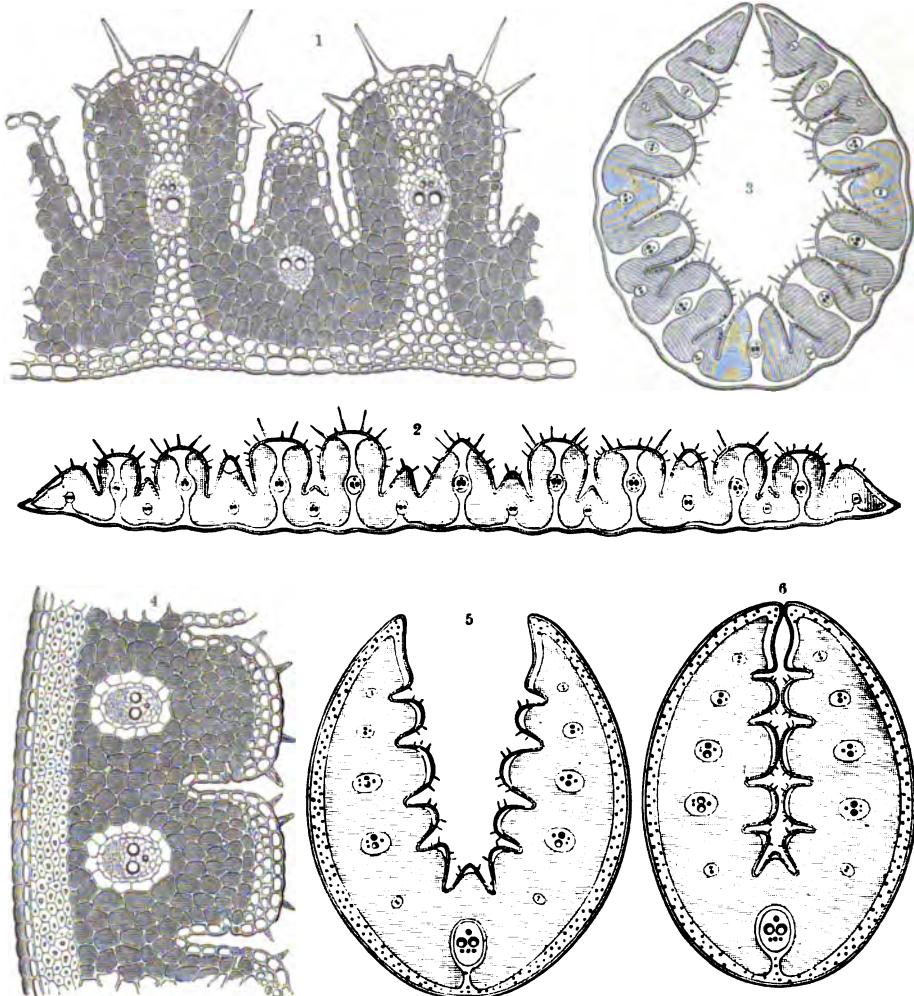


Fig. 86.—Folding of Grass-leaves.

- <sup>1</sup> Vertical section through part of the open leaf of *Stipa capillata*;  $\times 240$ .
- <sup>2</sup> Vertical section through an entire open leaf;  $\times 30$ .
- <sup>3</sup> Vertical section through a closed leaf;  $\times 30$ .
- <sup>4</sup> Vertical section through a portion of the leaf of *Festuca alpestris*;  $\times 210$ .
- <sup>5</sup> Vertical section through an entire open leaf.
- <sup>6</sup> Vertical section through a closed leaf;  $\times 30$ .

whose outer walls are much thickened. A vertical section through the leaf of *Festuca punctoria*, a native of the Taurus, is represented in fig. 88. In this plant, the leaves, when open, present a fairly shallow depression; the under surface is clothed with a protective mantle of five layers of strong cells devoid of chlorophyll; the ridges are rounded off and possess only a single layer of covering cells, provided with an extremely strong wax-like coat. The open leaves of *Festuca Porcii*,

a native of the Carpathians, are relatively thin (see figs. 87<sup>4</sup> and 87<sup>5</sup>). Below the epidermis of the under side is no mantle of bast cells as in the species already described, but only isolated strands of bast; however, the crest of each ridge is furnished with a strand of bast cells; the ridges themselves project very much, and the whole leaf is traversed by six deep narrow grooves.

In the three fescue-grasses cited here as examples, and in all species of the genus *Festuca*, forming the main part of the turf of our fields, a vascular bundle

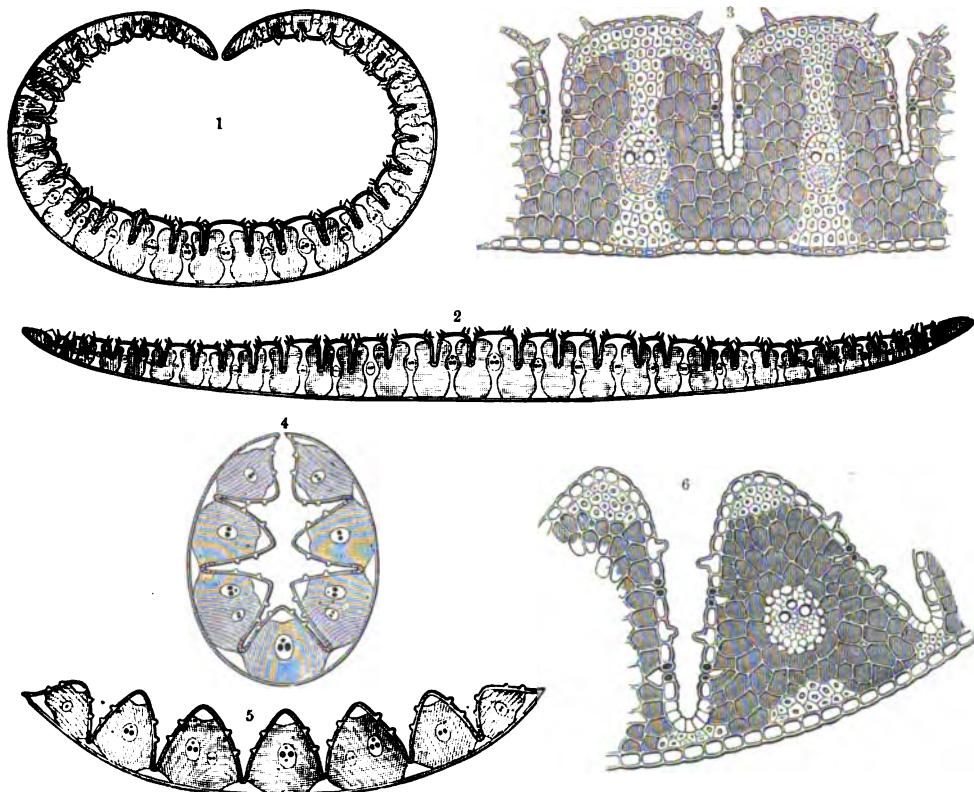


Fig. 87.—Folding of Grass-leaves.

- <sup>1</sup> Vertical section through a closed leaf of *Lasiagrostis Calamagrostis*. <sup>2</sup> Vertical section through an open leaf;  $\times 24$ .  
<sup>3</sup> Vertical section through a portion of the open leaf;  $\times 210$ . <sup>4</sup> Vertical section through a closed leaf of *Festuca Porcii*.  
<sup>5</sup> Vertical section through an open leaf;  $\times 24$ . <sup>6</sup> Vertical section through a portion of the open leaf;  $\times 210$ .

surrounded by green tissue traverses each ridge. In the hinged leaves of many other grasses, the green tissue of each ridge is divided into two portions. The vascular bundle is bordered above and below by strands of thick-walled cells devoid of chlorophyll, and thus arises a strong septum in the green parenchyma, beautifully shown in the transverse section of a leaf of *Lasiagrostis Calamagrostis*, illustrated in fig. 87. In the leaves of the Feather-grass (*Stipa capillata*) are alternating higher and lower ridges; a vertical section is shown in fig. 86<sup>1, 2, 3</sup>. In the higher ridges occur septa similar to those in *Lasiagrostis*, but in the lower there is only a vascular bundle surrounded by green tissue as in the fescue-grasses. No less than

twenty-nine ridges can be counted on the leaf of the above-mentioned *Lasiagrostis*, a plant widely distributed in the valleys of the Western and Southern Alps, where it clothes the sunny slopes in thick masses. When the leaf folds up, the twenty-eight grooves between the ridges, on whose sides are the stomata, become narrowed, and the entire leaf assumes a tubular form, so that transpiration is almost completely suspended. In *Stipa capillata*, which is very abundant on clay steppes, the same thing occurs (see fig. 86<sup>3</sup>). In both grasses the closure of the grooves on whose sides are the stomata, is completed by short stiff hairs on the summit of the ridges, which interlock when the ridges approach one another, and so block up access to the grooves (fig. 86<sup>3</sup>). It would take us much too far to describe the numerous other modifications which are to be met with in the structure of hinged grass-leaves. The examples given suffice to make it evident that the danger of over-transpiration is avoided by the folding of the leaf, and that amongst the grasses very many arrangements obtain in order, sometimes, to expose those green parts of the leaf whose epidermis is supplied with stomata to the rays of the sun, and at other times to withdraw them, according to the humidity of the soil and of the surrounding air, thus suitably regulating transpiration to the existing circumstances.

The mechanism by which grass-leaves open and close may be explained in two ways—either the process is due to hygroscopic changes, as in the opening and closing of the “Rose of Jericho”, or to alterations in the turgidity of certain groups of cells, as in the mimosas. If the former alone were the case, a dry, dead grass-leaf should be still capable of opening and closing in accordance with its damp or dry condition; but a leaf of any of these when cut off and dried no longer opens, even after being moistened for a considerable time, and therefore the first explanation cannot be accepted, at any rate for most of the grasses. Apparently, the mechanism consists of alterations in the turgescence of those groups of cells situated in the angle of the grooves. Since the floor of the grooves was frequently found to consist of peculiar thin-walled cells destitute of chlorophyll, and filled with colourless watery sap, it was concluded that the opening and closing of the grass-leaves was due to the change in turgidity of these cells. However, this was going too far. These cells in most instances, for example, in *Festuca punctoria* (see fig. 88<sup>2</sup>), would be much too delicate to effect, unaided, the closure of the leaf by their loss of turgidity, or to open it by their increasing turgescence. In many grasses these cells are completely wanting (e.g. in *Festuca alpestris* and *Stipa capillata*, fig. 86). Moreover, it is observed that the opening and closing of the leaf is still carried on when the thin-walled cells at the bottom of the grooves are destroyed, artificially, by puncturing with fine needles. The cause of the movement must therefore be looked for in the alteration of turgescence of other cells below the grooves. When a mantle of several layers of thick-walled cells is present on the under side of the leaf, their walls are seen to swell up simultaneously with the alterations of turgescence of the parenchymatous cells. Of course the inner cell-layers of the mantle must be capable of swelling up to a greater extent than the outer, and this has

actually been shown to be the case in some species. Moreover, although the thin-walled cells at the bottom of the furrows are not considered strong enough to bring about the opening and closing by changes in their turgidity alone, it is by no means asserted that they have no other part to play. When they are constructed as in the leaves of the moor-grasses and in the fescue-grass of the Taurus (*Festuca punctoria*, figs. 85 and 88), they certainly are not without a purpose. Their advantage to the plant lies in the fact that they can be much compressed without harm by the closure of the leaf, whereby the neighbouring parenchymatous cells are pro-

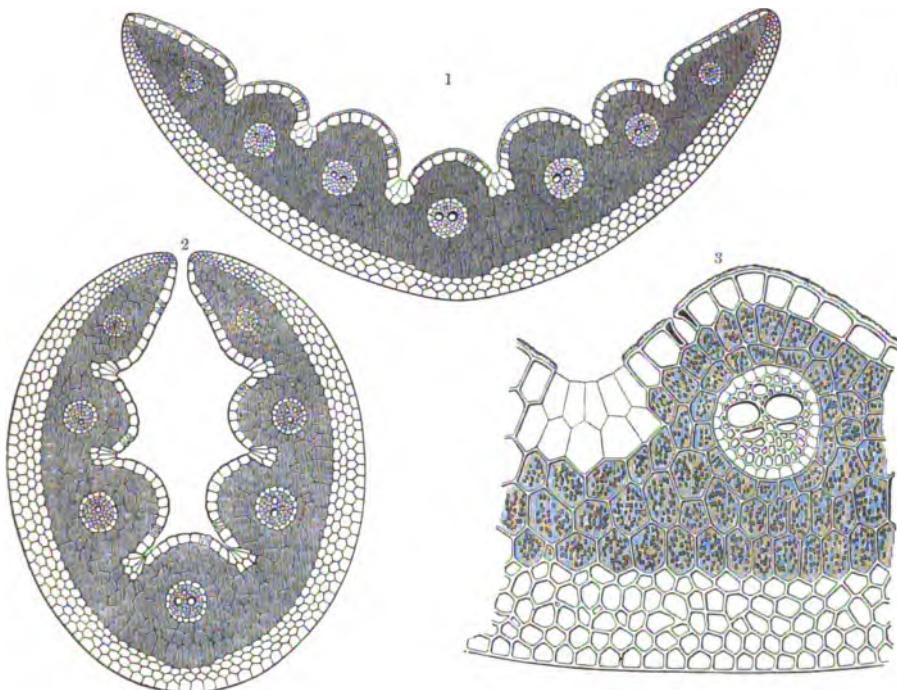


Fig. 88.—Folding of Grass-leaves.

<sup>1</sup> Vertical section through an open leaf of *Festuca punctoria*, of the Taurua. <sup>2</sup> Vertical section through a closed leaf;  $\times 40$ .  
<sup>3</sup> Vertical section through a portion of the open leaf;  $\times 280$ .

tected from injury; also that by means of these cells, which are filled with watery sap, carbonic acid from the atmosphere is conducted to the underlying green tissue; and lastly, that in case of necessity, water can be absorbed from the air. They remind one strongly of the thin-walled groups of cells of foliage-leaves used for the direct absorption of moisture, and possibly they can function in this way. If, in places where these grasses grow naturally, a slight shower of rain falls after a long period of drought, or if dew falls during clear nights, little or none of the water reaches the roots, since it is retained by leaves overspreading the soil. But the water easily runs into the furrows of the folded leaves of grass, and since the large thin-walled cells at the bottom of the grooves can be wetted, they offer to the water which can pass through them the shortest path to the green cells in the interior of the leaf.

A process, very similar to the opening and closing of grass-leaves, is also to be observed in the true mosses, in all species of the genus *Polytrichum*, and in some of the Barbulas. The peculiar structure of the leaves of these mosses has been already treated of. In addition to the description there given, it may be mentioned that the ridges of thin-walled green cells, which are present on the upper surface of such a leaf (see fig. 89), only remain exposed to currents of air as long as this air possesses the requisite degree of humidity; that is to say, the blade of the leaf from whose upper surface the bands project only remains expanded while that is the case (fig. 89<sup>2</sup>).

As soon as the air becomes dry, the lateral portions of the leaf-blade bend upwards, and envelop the green ridges like a mantle (fig. 89<sup>1</sup>). These are then

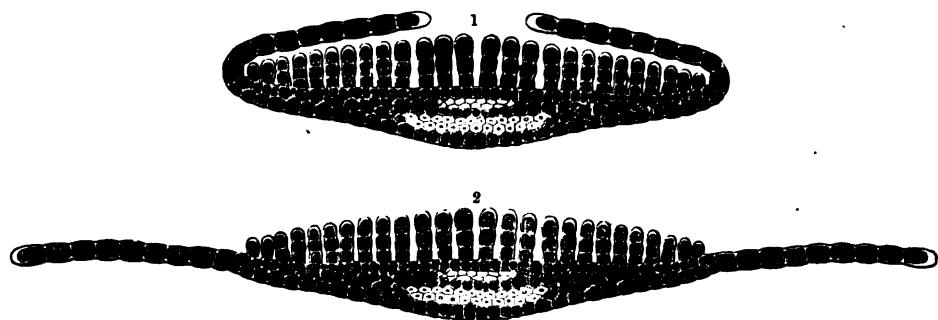


Fig. 89.—Folding of Moss-leaves.

Transverse sections through the leaf of a *Polytrichum* (*Polytrichum commune*). <sup>1</sup> The leaf dry and folded.  
<sup>2</sup> The leaf damp and open;  $\times 85$ .

inclosed in a hollow chamber, and only retain communication with the surrounding air by a narrow slit above, which is left open between the inflected leaf-margins. But here again it should be noticed that the highest cells in each ridge are strongly thickened on the part turned towards the opening, which doubtless helps to lessen transpiration. The opening and closing of the *Polytrichum* takes place very rapidly. By repeated hygrometric changes in the air, the process may be performed naturally several times in a single day. In *Polytrichaceæ*, which have been plucked while their leaves were open, the closure is seen to be completed, in dry air, in a few minutes. Dead and withered leaves are always closed, and never reopen, even when kept damp for a long time—from which it may be concluded that the mechanism of the opening and closing cannot be due to a simple hygroscopic phenomenon. Probably, the same mechanical forces come into action as produce the folding of leaves of grasses; but the process in moss-leaves is much more complicated, since it consists, not merely in the upward inclination of the leaf-edges, but also in an upward curvature and spiral twisting of the whole leaf.

#### 4. TRANSPiration DURING VARIOUS SEASONS OF THE YEAR. TRANSPiration OF LIANES.

**Old and Young Leaves.**—**Fall of the Leaf.**—**Connection between the structure of the Vascular Tissues and Transpiration.**

##### OLD AND YOUNG LEAVES.

The various regulators of transpiration, hitherto described, either persist in the plant-organs in question throughout life, or only remain for a comparatively short time. They are present throughout life in evergreen leaves, particularly in regions where wet and dry seasons alternate during the year. In this case the plants require powerful aids to transpiration in the rainy season, and in the dry season abundance of protective measures against excessive loss of water. Evergreen leaves cannot afford to dispense with either the promoting or inhibiting arrangements after the expiration of the first year, because for several years they still have to pass through both these seasons. It is otherwise with those leaves whose activity only lasts for a single summer. These burst from the buds at the beginning of the vegetative period, and then unfold, transpire and respire for a few months, producing organic materials, and conduct them towards the places where they are required. At the commencement of the drought, however, or on the appearance of frost, they turn yellow and fade, are detached from the stems and branches which bear them, and die. In leaves of this kind, an arrangement which is very necessary during the first season may become superfluous later—it may even become disadvantageous under changed external influences, and the leaf would then be benefited by freeing itself entirely from the contrivance. It would often be useful to the plant to substitute in the place of a protective contrivance, which is only beneficial at the commencement of the vegetative period, another arrangement fitted to the new and altered conditions. In the so-called deciduous leaves, *i.e.* in those which throughout the year are only active in the summer, often only for two months, it is a fact that an alternation of this kind may be regularly observed in the mechanisms which govern transpiration.

It will be noticed in a young foliage-leaf which has just pierced through the ground, or in one which is still half-hidden between the cotyledons of a seedling, or surrounded by the loosening scales of a winter bud, that the development of that portion whose duty will later on be to transpire and assimilate, is very backward. The leaf-veins are already very prominent, but the green tissue is in quite a rudimentary condition. It is not only that the extent of the surface is very small, but that the epidermis which covers it is not yet properly developed; the outer walls of the epidermal cells are not yet fortified with a cuticle, and are consequently neither water-tight nor impermeable to aqueous vapour. If exposed to sun or wind, the green tissue would at once dry up. When the young foliage-leaf has

forced its way out of the bud above the soil, or from between the cotyledons, the conditions are still the same, and therefore particularly efficacious protective arrangements are required that the leaves just merging from the bud, and thus exposed to the vicissitudes of the weather, may grow up properly, *i.e.* that their green transpiring tissue may be normally developed.

Some of these protective contrivances belong exclusively to the developing period of the leaves, and are lost when they become fully grown. Others may be seen in the adult leaves. The most striking instances are perhaps the diminution of the surfaces directly exposed to the sun and wind, the vertical inclination of the leaf-blades, and the concealment of the green tissue under a protective mantle.

The diminution of the surface directly exposed to the sun and wind is caused by the position which the foliage-leaf takes up within the bud. Space is very limited here, and the youngest and smallest leaves appear to be fitted into the space by the rolling, or folding, or crumpling of their blades. This diminution is obviously of great advantage when the leaves open out into the daylight: it constitutes a special protection against the drying up of the green tissues, and is, therefore, retained until other protective measures are developed, and in some cases even throughout life. In many Polygonaceæ (*e.g. Polygonum viviparum* and *Bistorta*), in species of Butter-bur (*Petasites*), in some Primulaceæ, and especially in many bulbous plants, the green portions of the leaf are rolled. The midrib, and frequently a fairly broad central strip of the leaf in addition, remains flat, and the right and left halves are rolled up from the margins, sometimes towards the upper, sometimes towards the lower surface. The stomata are chiefly, or wholly, to be found on the concave side, beneath which lies the soft green tissue with its ramifying air-passages. In the *Crocus*, the two halves of the leaf are rolled outwards; they are connected together by a broad, white, central stripe which is not rolled, and is devoid of chlorophyll; in the Star of Bethlehem (*Ornithogalum*), whose leaves are traversed by a similar white stripe, the leaf margins are rolled inwards. In species of *Crocus* the stomata are placed in the two grooves on the under surface; in the Star of Bethlehem, in the grooves on the upper surface. The central stripe of the young leaves in the plants mentioned always remains flat, but in young fern-leaves, which are also rolled, the strongly-developed midrib is curled spirally inwards like a watch-spring, and thus the green feather-like pinnæ, springing from the rachis, are placed one above the other. Most ferns in their native habitat rarely require special protection against over-transpiration during the first stages of development; but when this is necessary, it is afforded in every case by the form assumed by the young leaf just described. Moreover, in such instances special protective envelopes are, as a rule, to be found, which will be spoken of later.

Leaves are not so often crumpled as rolled on first emerging from the bud. In crumpled leaves the net-work of anastomosing veins forms a strong lattice-work, and the green leaf-substance, fitted into the interstices of the lattice, is swollen up like bubbles or sunken into pits, giving the whole leaf the appearance of a crumpled sheet of paper or cloth. The *vernation* (or position occupied by the leaf in the bud) is

therefore aptly termed "crumpled". Leaves specially noticeable in this respect are those of the many species of dock (*Rumex*), rhubarb (*Rheum*), and also of several spring primulas (*Primula aculealis*, *elatior*, *denticulata*, &c.). Frequently the crumpling and rolling occur together, leaves with crumpled vernation having their lateral margins also somewhat rolled inwards.

Young leaves which have just burst from the bud, and still retain the form they possessed there, are very often seen to be "plaited". The veins of the leaf form,



Fig. 90.—Unfolding of Leaves.

1, 2 Wild Cherry (*Prunus avium*). 3, 4 Walnut (*Juglans regia*). 5, 6 Wayfaring Tree (*Viburnum Lantana*).  
7 Lady's-mantle (*Alchemilla vulgaris*). 8 Wood-sorrel (*Oxalis Acetosella*).

as it were, the fixed framework, and it is only the green portions between which are laid in folds. From the multiplicity in form and division of the leaf-veins, the kind and manner of folding is also very varied. When the leaf-blade is traversed, by radiating veins, as, for example, in the Lady's-mantle (*Alchemilla vulgaris*), shown in fig. 90<sup>7</sup>, the leaf is folded in vernation just like a fan; the veins which radiate out in the adult leaf are as yet parallel to one another, and the green portions which in the fully-formed leaf are stretched between the veins, form deep folds, which are closely packed together. The same arrangement occurs when each of the radiating

veins becomes the midrib of a leaflet, as in the cinquefoils, and species of clover and Wood-sorrel. Each leaflet is folded up along the midrib like a sheet of paper, and the folded leaflets are placed side by side in the same way as folded leaves in a book.

When the leaves are pinnate, and the leaflets are arranged in pairs on a common rachis, the latter are folded together along their midribs, and placed side by side, so as to resemble the pages of a book. This vernation occurs in roses, Mountain Ash (*Sorbus aucuparia*) and Walnut (*Juglans regia*), see figs. 90<sup>3</sup> and 90<sup>4</sup>. In the roses the rachis is so short in the bud that the leaflets springing from it appear to originate from one point, as in the cinquefoils. In most maple-leaves and those of *Saxifraga peltata*, the folding takes place not along the radiating veins alone, but along the short lateral veins which spring from the larger radiating ribs. In this way small folds are inserted between the larger, and this vernation leads up to that which was described before as "crumpled". The leaf-folding exhibited by the foliage of the Beech (*Fagus silvatica*, see fig. 92), the Hornbeam and the Hop-hornbeam (*Carpinus* and *Ostrya*), the Oak (*Quercus*), and many other plants, whilst in the bud, is very characteristic. Each foliage-leaf possesses a midrib and numerous strong lateral veins, which run right and left from the midrib like the bony processes from the spinal column of a fish. The green portions of the leaf form deep folds between these lateral veins, which are as yet very close to one another, and the folds are thus arranged exactly as in a fan. Yet another method of folding occurs in the Cherry (*Prunus avium*). Each leaf, while in the bud, and for some time after it has burst from it, is folded along the midrib only (see figs. 90<sup>1</sup> and 90<sup>2</sup>). The right and left halves are so flatly folded together, and fit over one another so completely, that at first sight they appear to form only a simple leaf-blade. Moreover, the two halves which are in contact are actually joined by means of a balsam-like secretion. At this stage of development they are always erect; and this brings us to another protective contrivance to be observed in young undeveloped leaves.

It may be stated that, with the exception of a few "crumpled" forms, all young foliage-leaves when they emerge from the bud-scales, or from between the cotyledons, or as they force their way through the soil into the light of day, are so directed that their blades are not horizontal. In this first stage of development, indeed, the green transpiring, but still delicate, portions of the leaf have always a vertical position. Their blades usually exhibit the direction observed in phylloclades and phyllodes, in the equitant leaves of irises and tofieldias, in the leaves of the compass plants during their greatest activity, and in the leaves of grasses when folded together in dry air. Sometimes the entire extended or rolled blade is erect, as in most bulbous plants and grasses; or the midrib is inclined towards the horizon, in which case the halves of the leaf are folded together and the two margins come into contact, forming a sharp edge which is turned towards the sun at noon. This is seen in some grasses (*Glyceria*, *Poa*), and in the Cherry (*Prunus avium*). If the blade is not erect, the stalk of the leaf is perpendicular while the

still delicate blade hangs from it like a closed parasol, as in *Podophyllum*, *Cortusa*, *Hydrophyllum*, and several Ranunculaceæ. In the Horse-chestnut (*Aesculus Hippocastanum*) the folded leaflets are erect when they emerge from the bud; they then sink down so that their apices point to the ground; and later, when the epidermis has become more thickened, they again rise until they are almost horizontal. Leaves of limes (*Tilia grandifolia* and *parvifolia*) are vertical when they first break through the bud, the apex directed towards the ground; it is only later that they become almost parallel with its surface. The upright leaf-stalk is often bent like a hook at the end, and the vertical folded leaflets depend from the hooked portion. This arrangement is shown in the common Wood-sorrel, and many other plants (see fig. 90<sup>s</sup>).

A third method of protecting these delicate undeveloped green portions of young leaves consists in the formation of screens and coverings, which exhibit the greatest variety. The envelope is frequently furnished by the so-called *stipules*. In many plants two lobes arise on the right and left of the leaf-stalk at the point of junction of the leaf and stem, and these have been termed "stipules" (*stipulae*). In figs, oaks, beeches, limes, magnolias, and numerous other plants, the stipules are membranous, pale, usually without chlorophyll, and they appear like scales placed as screens in front of the small, tender green leaflets when they burst through the bud, and in any case must be considered to protect them from the sun's rays (see fig. 92). When once the young leaf has grown beyond the top of these screens and no longer needs them, they shrivel up, are detached, and fall to the ground. Millions of such fallen scales, called in botanical terminology "deciduous stipules", are to be seen on the ground in oak and beech forests shortly after the leaves have attained their normal size. The stipules of magnolias, particularly of the Tulip-tree (*Liriodendron tulipifera*), a native of North America, but now cultivated all over Europe, are very remarkable (see fig. 91). They are comparatively large and boat-shaped, and are always so arranged in pairs as to form a closed cup. Shut up within this membranous, slightly transparent cup can be seen the young leaf, its stalk being bent into a hook, and the two halves of the blade folded together along the midrib like those of the Cherry. In this position the leaf grows gradually as if in a small greenhouse; it enlarges, and as soon as the epidermal cells are so much thickened that there is no further danger of it drying up, the cup opens and the two boat-shaped stipules separate from one another, shrivel up, and at length fall off. Only two scars at the base of the leaf remind one that two stipules were situated here in the spring, whose function was to protect the delicate young leaf from desiccation.

One of the most noticeable arrangements for the protection of the tender, undeveloped green tissue consists in the peculiar grouping of the leaf-veins. This may be best observed in foliage-leaves which are folded along the lateral veins in vernation. Each individual leaf is erect, usually a little bent at the apex and margins, and slightly hollowed so that the upper surface is concave, and the lower side, which is turned towards the incident light, convex. Since the midrib of the

leaf is still comparatively short, while the numerous lateral veins, on the contrary, are already strongly developed, the latter must lie so close to one another that they actually come into contact. Consequently on the under surface of the erect leaf, which is turned towards the sun, nothing can be seen of the delicate green tissue;



Fig. 91.—Leaf-unfolding of the Tulip-tree (*Liriodendron tulipifera*).

<sup>1</sup> A twig at the end of which the leaves are beginning to unfold. <sup>2</sup> End of the same twig, the leaves being further expanded.  
<sup>3</sup> The anterior boat-shaped stipule artificially removed from the upper bud. <sup>4</sup> One of the stipules about to fall off.

only the thick lateral veins, devoid of chlorophyll, stand out side by side like the supporting framework of a rush mat. The green portions of the leaf, which extend between the veins, form projecting folds on the concave surface, i.e. on the surface which is turned from the sun. They are thus hidden behind the close-pressed layer of ribs as if by a roof, and are consequently protected as efficiently as possible from

the sun and wind. The ribs themselves are composed of cellular structures which are not open to the danger of over-transpiration, and the epidermis which covers them is entirely devoid of stomata. When the leaves at the ends of the young twigs are opposite, erect, and concave, and their margins are in contact, they form an actual capsule round the apex of the shoot. This occurs in the Wayfaring Tree (*Viburnum Lantana*), illustrated in fig. 90<sup>5</sup>. The small folds of green tissue project into the interior of the capsule, and the still closely-pressed lateral veins form the outer wall, and at the same time furnish a protective covering for the enlarging green portions of the leaf. As soon as these are fully developed, and the



Fig. 92.—Unfolding of Beech-leaves.

- <sup>1</sup> The brown bud-scales have been loosened, and the membranous stipules surrounding the foliage-leaves are visible above.
- <sup>2</sup> Further stage of development, the folded foliage-leaves being visible between the stipules. <sup>3</sup> The same twig further developed.
- <sup>4</sup> Lower surface of a young folded leaf. <sup>5</sup> Portion of the same leaf; the depressions caused by the folding are bridged over by silky hairs.
- <sup>6</sup> Surface view of an unfolded leaf; the stipules are withered and about to fall.
- <sup>7</sup> Vertical section of a leaf at right angles to the midrib. <sup>8</sup> Vertical section parallel with the midrib.

epidermal cells are correspondingly thickened, the projecting folds become smooth, the veins separate from one another, and the whole leaf becomes flat, assumes a horizontal instead of a vertical position, and turns the upper instead of the lower surface to the incident light (see fig. 90<sup>6</sup>).

It has already been repeatedly stated that coats of varnish as protective coverings are especially to be met with on young leaves, which they guard from over-transpiration and desiccation during their development, and that when the leaf-laminae become provided with a cuticularized epidermis, these coats disappear. It has also been pointed out, incidentally, that coats of hairs are of great use as protections and screens to the young foliage-leaves when they first emerge from the

buds. The leaves of a great number of plants are only hairy during the commencement of development. Long hair-cells may be seen inserted by their narrow bases between the flattened epidermal cells; these at an early stage shrink up close to their origin, and then break off. They may remain hanging to the leaf for a little while, but afterwards are thrown or pushed off by the enlargement and expansion of the leaf-blade, or are frequently blown away by the wind. The leaflets, which were originally quite thickly clothed with hairs, then appear partially or entirely smooth and green on both sides. A remarkable instance of this is furnished by *Amelanchier vulgaris*, whose foliage, early in the spring, is folded along the midrib and covered with snow-white wool, reminding one strongly of the Edelweiss, while in the summer no trace of the covering remains. The White Poplar (*Populus alba*), pear-trees, and mountain-ashes behave in like manner. Horse-chestnut leaves, when they make their way through the brown, loosened bud-scales, are thickly covered with wool, but during the spring they lose this so completely that only here and there on the fully-formed leaves can remnants still be observed clinging to the leaf. It is, however, not only woolly coverings that are later either partially or wholly thrown off as superfluous. On the foliage-leaves of the already-mentioned Wayfaring Tree (*Viburnum Lantana*) appear felted stellate hairs which fall off as soon as the epidermis is sufficiently thickened. In a species of Rhubarb (*Rheum Ribes*) brittle, candelabra-like, short-branched trichomes are situated on the edge of the leaf, which is much crumpled at an early stage, and later, when of no further use, they break away in pieces and fall off. Again, in many mulleins (e.g. *Verbascum pulverulentum* and *granatense*), there are branched, shrub-like hair-structures which become detached from the surface of the fully-developed leaves, and are carried away in loose flakes by the wind.

The covering of the young leaves of the Beech (*Fagus sylvatica*) consists of silky hairs, and the way in which these are arranged and utilized is so peculiar that it is worth while to inquire further into the details. At first sight, the under surface of the young beech-leaf appears to be entirely covered with silky hair; on a closer examination, however, it is seen that the hairs are only inserted on the margins and on lateral veins, and that the green portions of the leaf are in reality perfectly smooth and free from hairs. Since the green portions of the leaf are thrown into deep folds (see figs. 92<sup>4</sup> and 92<sup>5</sup>), and the veins are still close to one another, while the tops of the silky hairs springing from these veins reach far beyond the vein next to them, all the furrowed depressions caused by the folding are completely covered over. Each groove is bridged over by the hairs, which are regularly arranged, side by side, parallel to one another; thus the leaf appears to be clothed completely in a delicate silken coat. There can be no doubt as to the function of these hairs. The green tissue overspanned by them is protected from the sun until its epidermis is sufficiently thickened, and when this is the case the folds flatten out (fig. 92<sup>6</sup>) and the leaf assumes a horizontal instead of a vertical position, thus turning the lower surface away from the sun, and rendering the hairs of no further use. They have become

superfluous, and usually fall off—or, if they still remain on the lateral veins, they are shrivelled, insignificant, and meaningless.

The dry membranous scales seen on young fern-leaves should be mentioned here. Let us examine a frond of the first wild fern we meet—say of *Nephrodium Filix-mas*. The young frond is still spirally rolled, although it has forced its way through the soil, and is now exposed to the wind. Moreover, nothing is to be seen of the fresh green which later adorns this fern; the lower part of the midrib and lateral veins appear to be strewn with chaff, being entirely covered with dry membranous brown scales and shreds. Later, as the leaf unrolls more and more, its green fronds also become expanded, but by this time the cell-walls are sufficiently strengthened, and no longer require the chaffy coat. In ferns which grow in sunny, rocky situations, and as epiphytes on the fissured bark of old trees in tropical regions, this coat of chaffy scales is even more noticeable, and, as stated earlier, in such plants it persists throughout life.

#### FALL OF THE LEAF.

Just as many phenomena of the sprouting and unfolding of foliage are dependent upon transpiration at the beginning of the vegetative period, so many processes, but chiefly that of the fall of the leaf, stand in causal connection with transpiration at the close of that period. Sooner or later, of course, the activity of each leaf entirely ceases; it dies, becomes detached from the stem to which it has rendered service, and falls to the ground, where it decays. In districts where the vegetation can continue its activity uninterruptedly throughout the year, there is nothing very noticeable about the fall of the leaf. As a rule, as the new leaves arise below the growing apex of the shoot, the lower, older leaves wither up and decay; the fall is quite gradual, and takes place, like the development of new leaves, all through the year. In neighbourhoods, however, where the changes of climate prevent the uninterrupted activity of plants throughout the year, it is essentially different. Trees and shrubs, and many smaller plants, shed the whole of their foliage in a few days at certain annually-recurring periods, and then remain with bare branches for a considerable time, apparently quite lifeless. This is the case in regions where a long, hot, dry period follows the short rainy season, and also in very cold districts where the long-continued frost causes an icy winter, and the plants are locked in a deep sleep. In tropical and sub-tropical regions, where no showers occur for many months at a time, the branches become stripped of their leaves. Even at the beginning of the dry hot season, they remain apparently dead for months, but again break out into leaf at the commencement of the cooler rainy season, when invigorating moisture is supplied to the parched ground. On the other hand, in those regions of the temperate zone in which there is no sharp distinction between the rainy and dry seasons, and rain falls every month, the foliage is stripped from the trees at the beginning of the cold period, and after the winter is over, fresh green leaves once more burst from the buds on the branches.

It certainly appears strange that the leaf-fall should be sometimes connected with the approach of cold, and sometimes with that of hot weather. And yet this is the fact. Heat and cold are only the indirect causes; the primary cause of the fall of the leaf is the danger threatened to the plant by the continuance of transpiration when either heat or cold is excessive. The danger of transpiration during continued dryness of soil and air scarcely requires much explanation. The conditions may be summed up in a few words: the throwing off of the transpiring surfaces when the drought commences, and the temporary stoppage of the sap-current—*i.e.* the so-called “summer sleep”—furnish one of the best protective measures in plants surrounded by air against excessive transpiration and withering. It is more difficult to explain the connection between the fall of the leaf and the commencement of the cold period. This is best indicated by some culture experiments which illustrate these relations. When the soil, in which are cultivated plants with actively transpiring leaves (melons, tobacco, and the like), is cooled down to a few degrees above zero, the leaves after a short time become faded, even although the temperature of the air and the humidity of both soil and air are entirely favourable. By the lowering of temperature in the soil, the absorbing activity of the roots buried therein is so reduced that the water which is lost by transpiration from the foliage-leaves can no longer be replaced. The leaves wither, dry up, turn brown or black, and appear to be burnt or charred. In the ordinary language of gardeners they are said to be “frozen”—frozen at a temperature above the freezing point, which phenomenon is said to be due to the peculiar sensitiveness of these plants. It is incorrect to speak of freezing in this case, however. The plants are in reality dried up by reason of the low temperature of the soil and consequent lessening of the stream of fluid up to the transpiring foliage-leaves. In regions which annually pass through a long period of cold, the leaves of the plants are as liable to be dried up by the cooling of the soil round their roots when winter approaches, as are the trees in the catingas of Brazil when the hot dry season commences. They also denude themselves of their leafy raiment as these do, since otherwise they would be unable to make good the water exhaled by the leaves. When the temperature of the air sinks below zero, frost ensues, and the water in the plant stiffens into ice; this hastens the fall of the leaf, but it was already partially accomplished before the frost set in, and where the leaves still cling to the branches, preparations are already made for their detachment, which is brought about by the limitation of transpiration. It must not be concluded from this that plants foresee the approach of winter, and that the preparations for the fall of the leaves result from such an intelligent foresight; the phenomenon is much more easily explained on the assumption that in a climate which renders necessary a long cessation of transpiration, those plants flourish and multiply best whose natural characteristic is to follow a period of energetic work by a long season of rest. The ultimate cause of this instinctively adaptive periodicity is certainly not yet explained; it is as mysterious as those life processes and phenomena which regularly recur at certain periods, which are perhaps hastened or retarded by favourable or unfavourable external conditions, but cannot

be stopped by them, and which the plant carries out, or endeavours to carry out, without immediate external stimulus.

It is highly interesting, with respect to the acceleration or retardation of the leaf-fall, to observe how the same species of plant will behave under various favourable or retarding external influences; or how, in each region and locality, a selection has been made to a certain extent of the plants best adapted to the given conditions. First it is to be noticed that, under otherwise similar circumstances, the foliage remains green for a longer time, and is retained longer on the branches in places where the soil and air are more humid. In damp, shady, wooded glens, not only ferns, but the leaves of birches, beeches, and aspens are still green while on the sunny hillocks close at hand the brown leaves flutter down on to the withered fronds of the Bracken Fern.

The most remarkable fact, however, is that in elevated mountain regions a plant loses its leaves much earlier than does the same species growing in the lowlands. From the fact that in the Alps, the larches and whortleberry bushes, on the upper limits of the woods, put forth their green needles and leaves about a month later than in the valleys at a height of 600 metres above the sea, it would naturally be expected that this considerable delay would be compensated for by a corresponding postponement of the ending of the year's work, and that the fall of the foliage on the upper limits of the wood would also be postponed for about a month. But this is far from being the case. The same species of larch which becomes green a month later, up on the mountain slopes, also turns yellow a month earlier in the autumn. While the whortleberry bushes in the depths of the valley are still adorned with dark-green leaves, the same species growing in the glades on the upper limit of the wood, already, from the valley, appear to be shrouded in deep crimson. Their leaves are becoming discoloured above, and are withering and dropping from the twigs. The explanation of this phenomenon follows naturally from what has just been said. In the high mountain regions where tall trees find their uppermost limit, the ground is frequently covered with frost at the end of August; snow falls regularly in the first half of September, and although this may be melted in sunny places, the soil is nevertheless thoroughly cooled by the water so produced. The days rapidly become shorter, and the sunbeams can no longer replace the heat lost by radiation in the lengthened nights. The temperature of the soil in which the plants are rooted consequently falls rapidly, and the immediate results are that the absorbent roots stop working, the decolorization progresses, and the foliage-leaves, which are no longer able to repair the loss caused by transpiration, wither and fall away. Accordingly, on this upper tree limit, only those larches and whortleberry-bushes can thrive which are organized to commence their year's work a month later, and to finish it a month earlier, than those which have taken up their position 1400 metres below.

This obviously applies not only to the larches and whortleberries, cited here as examples, but to all other plants whose range of distribution extends from the lowlands up to the wood limit on the slopes of the mountains. It also applies

further to those plants which have a wide horizontal distribution; for example, to those which grow wild or are cultivated from the lowlands at the northern foot of the Alps to South Italy, and even further south, on the further side of the Mediterranean. By journeying southwards, it will be seen that the beeches and elms which, on the northern foot of the Alps near Vienna, lose their colour in the beginning of October, are never discoloured before November on the mountains of Madeira, and that whilst the planes already show leafless branches in the North Tyrolese valleys at Innsbruck, they retain their leaves (although these are turning yellow) on the mild shores of Lake Garda at the southern foot of the Alps. In Palermo they are still adorned with dark-green foliage. Planes, indeed, in certain instances remain green all winter in Greece, and thus far it was no myth when Pliny spoke of evergreen planes. The Elder, which in the north is a deciduous plant, in Poti, on the Black Sea, retains its green leaves through the whole winter. In the oases of the North African deserts the Peach-tree keeps its foliage fresh and green from one vegetative period to another, and while the blossom of this tree in Central and South Europe unfolds on branches which have lost their foliage in the previous autumn, in the oases the flowers are situated amongst the still green leaves of the last period of vegetation. It may be confidently assumed that here also the cause is the temperature and humidity of the ground, and that the planes and peaches, whose roots at the end of autumn and winter are buried in a damp and relatively warm soil, are the last to throw off their foliage.

From all these considerations it cannot be doubted that the stripping of the foliage depends upon the stoppage of transpiration, and primarily upon the drying-up of those sources from which the transpiring leaves derive their water. Plants which denude themselves of their foliage of course lose with it much organic material, for whose production they have toiled for months; but this loss will stand no comparison with the advantages gained by the abscission of the leaves. In reality, it is only a framework of empty cells—the dead envelopes of the living portion of the plant—which is thrown away. The protoplasm has opportunely withdrawn, the plastids which carried on their activity in the cells of the foliage have migrated thence and taken up winter quarters in other sheltered parts of the plant—in the stem, roots, or tubers, and have there deposited everything which will be of use in the following year, such as starch, sugar, &c. The empty cells can thus be easily sacrificed to the common weal. The leaves fall to the ground, where they decay and help to form natural mould, of which the posterity of the deciduous plants reap the benefit. Since, by the formation of albuminous compounds in the leaves, an abundance of calcium oxalate arises which is of no further use to the plant, and is consequently stored up in such quantity at the end of summer that it at last becomes burdensome to the plants, the throwing off of the foliage must really be regarded as a method of removing waste materials, and may be compared to the excretion of waste which occurs in animals.

Finally, it should be noted that only plants whose foliage lies flat on the ground, or whose branches and twigs are very elastic and bear needle-shaped leaves, are

unharmed by the pressure of snow. Trees, bushes, and shrubs with broad out-spread leaves, such as planes, maples, limes, beeches, and elms, are not capable of supporting the weight of snow lying on their large leaf-surfaces. When, as occasionally happens, mountain and valley are covered in snow in the autumn before the leaf-fall has commenced, or when, late in the spring, to the terror of the farmer, snow falls on wood and meadow after the young leaves have attained to a considerable size, the devastation produced is fearful. The large-leaved shrubs are pressed down and their stems broken. Branches as thick as one's arm and huge tree-trunks are shattered, and in the woods quantities of maples and beeches are felled, or even uprooted. Such devastation would recur every year in regions with snowy winters if the leafy trees did not strip off their foliage in time, and it can easily be imagined what would happen to the woods after a series of such catastrophes.

There is, consequently, a widespread idea that the autumnal leaf-fall is brought about by frost. This idea is founded on the observation that when the temperature in October and November falls below zero, quantities of leaves drop from the branches in the early hours following the cold bright nights. Though it can scarcely be denied that the fall of the leaf is in some measure connected with frost, still that it is not always the immediate cause, is demonstrated by the fact that when plants with leafy branches are exposed at the end of August or beginning of September to a temperature below zero the leaves do not fall immediately; while, on the other hand, the foliage of limes, elms, maples, cherry-trees, &c., is at last stripped off in the autumn even though no frost has occurred. It can only be said, therefore, as already stated, that frost is favourable to the fall of the leaf, and that it hastens the commencement of the process; but not that the detachment of the foliage is brought about by its sole agency.

The detachment of the leaves from the branches is brought about by the formation of a peculiar layer of cells, from the co-operation of a special tissue, which has been termed the *layer of separation*. As a rule, leaves cannot detach themselves without the previous formation of this tissue, not even if they are exposed for a long time to a very low temperature, and the sap in their cells and vessels is stiffened into ice. That portion of the leaf in which the separation is to take place is made up of a strong tough tissue, and the mechanical alterations produced by the frost would not suffice to complete the rupture. The separation-layer, on the other hand, which is formed within this tissue in one or several definite places, consists of succulent parenchymatous cells, whose walls are so constructed that they are easily separated by mechanical or chemical agencies, thus rendering possible a disintegration of the cell-tissue. The incitement to the construction of a layer of separation is indeed usually the limitation of transpiration by the gradual cooling of the ground, and the cessation of the absorbing power of the roots in those regions which experience a cold winter. As soon as this restriction of transpiration commences—and it varies very much, as shown in the previous discussion, with the latitude and altitude of the region in question—thin-walled cells arise in the lower

portion of the leaves and leaflets, which rapidly increase by division, and in a short time form a zone, readily to be distinguished from the thick older tissue by its lighter tint and by the fact that it is somewhat transparent. Usually this zone is formed in the petiole, and at those places where the vascular bundles become narrowed in passing from the twig to the leaf-blade, there to divide up into the ribs and veins. The growing tissue is inserted just at this place; it actually presses and tears the other older cells apart, and even causes a rupture between them. As soon as the separation-layer has attained its proper thickness, its thin-walled cells separate from one another, but so as not to injure or burst their membranes in any way. It seems that the so-called middle lamella of the cell-wall is dissolved by organic acids, and that thus the continuity between the cells of the separation-layer is destroyed. The most trifling cause will now effect a splitting in the loose tissue and a fracture between the cells of the separation-layer; and when no other external shock follows, the detachment ultimately takes place of itself, the weight of the leaf helping to bring about a complete severance. As a rule, however, the fall of the leaf is hastened by external influences. Every gust of wind brings down the leaves; the alterations in volume dependent on the frost and chill and the subsequent thawing of the cell-sap, aid the severance and also hasten the tearing of vascular bundles which are still entire; and thus it happens that thousands of leaves fall to the ground even in the absence of wind, especially when, after a frosty night, the rising sun illuminates the autumn-tinted leaves, and dissolves the frozen sap.

The region where the separation is effected is usually sharply marked off, and it looks as if the leaves and leaflets had been cut through with a knife. The severed surfaces present a variety of contours, according to the shape of the leaf-stalk. Sometimes it is horseshoe-shaped, sometimes triangular or rounded, or it reminds one of a trefoil-leaf, and sometimes it has an annular shape. The stalk of the plane-tree leaf has at the base a conical swelling which incloses a bud; when the leaf falls a fissure is formed entirely going round it. Many of the separation surfaces of the leaf-stalks are like the articular surfaces of the long bones in the human skeleton (of the radius, tibia, and at the elbow). Vine leaves form two layers of separation, one close to the stem at the base of the leaf-stalk—the other at the upper end of the leaf-stalk immediately below the blade. In the palmate leaves of the Horse-chestnut and Virginian Creeper (*Ampelopsis*), in the compound leaves of *Spiraea Aruncus*, in the pinnate leaves of the Chinese Tree of Heaven (*Ailanthus glandulosa*), and in the bipinnate leaf of the North American *Gymnocladus Canadensis*, a small separation layer arises below each leaflet, and a larger one, in addition, at the base of the leaf-stalk. Such leaves, consisting of several leaflets, collapse like houses built of cards when touched, and under the trees late in the autumn lies a confused heap of leaflets and leaf-stalks, the latter sometimes looking like long rods (as, for example, in the *Ailanthus* and *Gymnocladus*), sometimes almost like long bones (as in the Horse-chestnut, fig. 93).

Frequently the layer of separation is so situated on the leaf-stalk that after the

detachment a small portion of the stalk remains on the branch. This is the case in the so-called Syringa, or Mock Orange (*Philadelphus*), where the scale-like part which is left has to protect the bud situated just above the leaf-stalk.

In some trees and shrubs defoliation is very rapid, in others only gradual. In the Japanese Maidenhair Tree (*Ginkgo biloba*), the formation of the separation-layer and the detachment of the leaves is completed in a few days; in hornbeams and oaks the stripping of the foliage continues for weeks, and frequently only a portion

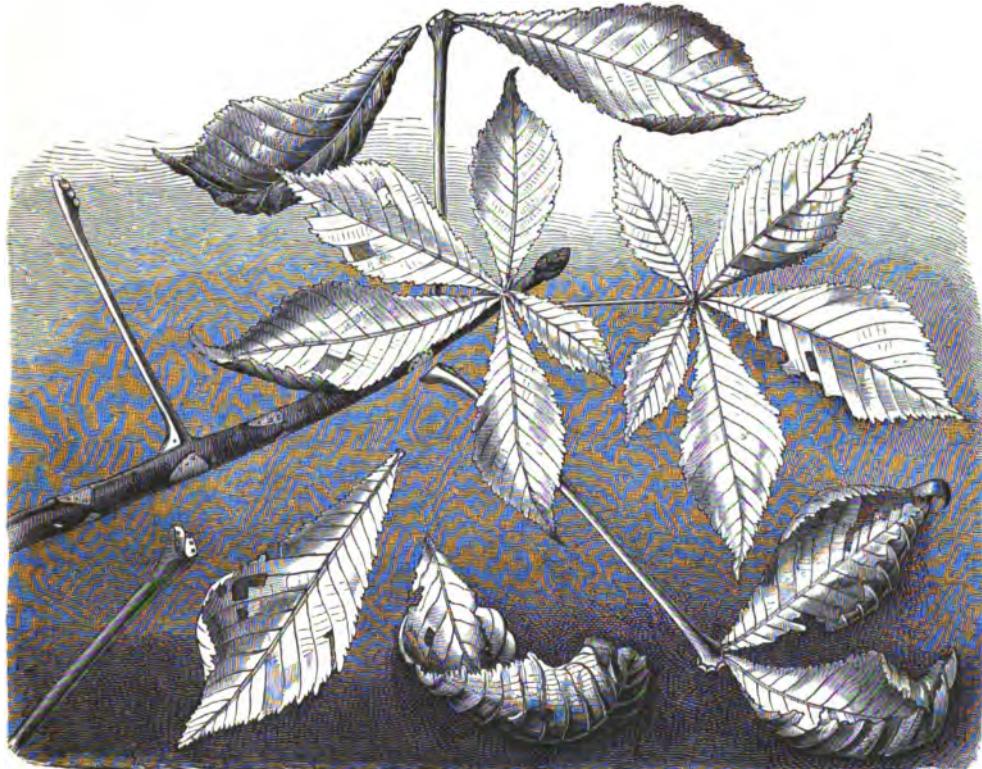


Fig. 93.—Leaf-fall of the Horse-chestnut (*Aesculus Hippocastanum*).

of the dead leaves is thrown off in the autumn, the remainder not until the close of the winter.

It is also worthy of remark that in some trees the leaf-fall begins at the end of the branches and gradually proceeds towards the base, while in others the contrary is the case. In ashes, beeches, hazels, and hornbeams, the apices of the branches are leafless when the lower parts still bear firmly-fixed foliage; in limes, willows, poplars, and pear-trees, on the other hand, the lower portions of the branches are seen to lose their leaves early in the autumn, the denudation gradually extending upwards; on the extreme ends of the branches some leaves, as a rule, obstinately remain for a long time, until they also are at length whirled away by the first snowstorm.

#### CONNECTION BETWEEN THE STRUCTURE OF THE VASCULAR TISSUES AND TRANSPIRATION

It is naturally to be expected that between the contrivances regulating transpiration in the immediate neighbourhood of the green tissue, and those mechanisms which effect the transport of the crude sap from the roots, through the stem and branches, up to the region of this transpiring tissue, a mutual co-operation will exist.

Where much water is exhaled from the surface, much water must be supplied, and in tracts leading to extensive and strongly-transpiring leaf-blades, the fluid moves more quickly than in a conducting apparatus leading to green tissue, which transpires but slowly and to a small extent. In pines, whose stiff acicular leaves transpire but little, the raw food-sap moves much more sluggishly than is the case with maples, whose flat leaves give off large quantities of water in the form of vapour. The quickest movement, however, is to be found in twining and climbing plants, whose stems, a few centimetres in thickness, may attain to a length exceeding 100 metres. This is the case in those peculiar climbing palms, which at first wind over the ground in numerous snake-like coils, and then rise to the tops of the highest trees, and unfold their leaves there in the sunshine. Climbing palms (Rotang) are known whose stems actually attain a length of 180 metres, and which, when they have reached the summit of the trees after numerous windings, become erect and extend their larger pinnate leaves just like the straight-stemmed palms. The illustration opposite (fig. 94) depicts in the background the edge of a wood up whose trees have climbed examples of such a species of Rotang.

Many hours of the day may pass, when, on account of a clouded sky and the great humidity of the air, the transpiration in the wide-spreading leaves above the tops of the trees will be extremely little; but when the sun shines brightly and the leaves become thoroughly warmed, a large quantity of water vapour must be exhaled in a very short time. This quantity of water must be replaced, and very quickly, but by means of a stem 180 metres long and only some centimetres thick. In order to render the replacement possible, everything which might hinder the rapid movement of the water and its dissolved food-stuffs on its long journey, especially the resistance of the conducting tubes, must be minimized as much as possible. The forward movement of fluids in a channel is, however, rendered more difficult as the tube narrows, because in a narrower tube a relatively larger amount of the fluid adheres to the inner surface, and therefore it is necessary, in order to obtain a rapid movement, that this adhesion be reduced as far as possible. This is most simply effected by widening the channel, since the adherent surface is thus diminished in comparison with the large amount of the fluid passing through. As a matter of fact, in the stems of climbing palms relatively very wide tubes are to be seen, through which a large quantity of fluid can be brought from the roots to the transpiring leaf-surfaces in a very short time, and this actually occurs. The climbing palm, *Calamus angustifolius*, has conducting tubes

of more than  $\frac{1}{2}$  mm. diameter, and in the species of Rotang illustrated in fig. 94 they are almost as wide.

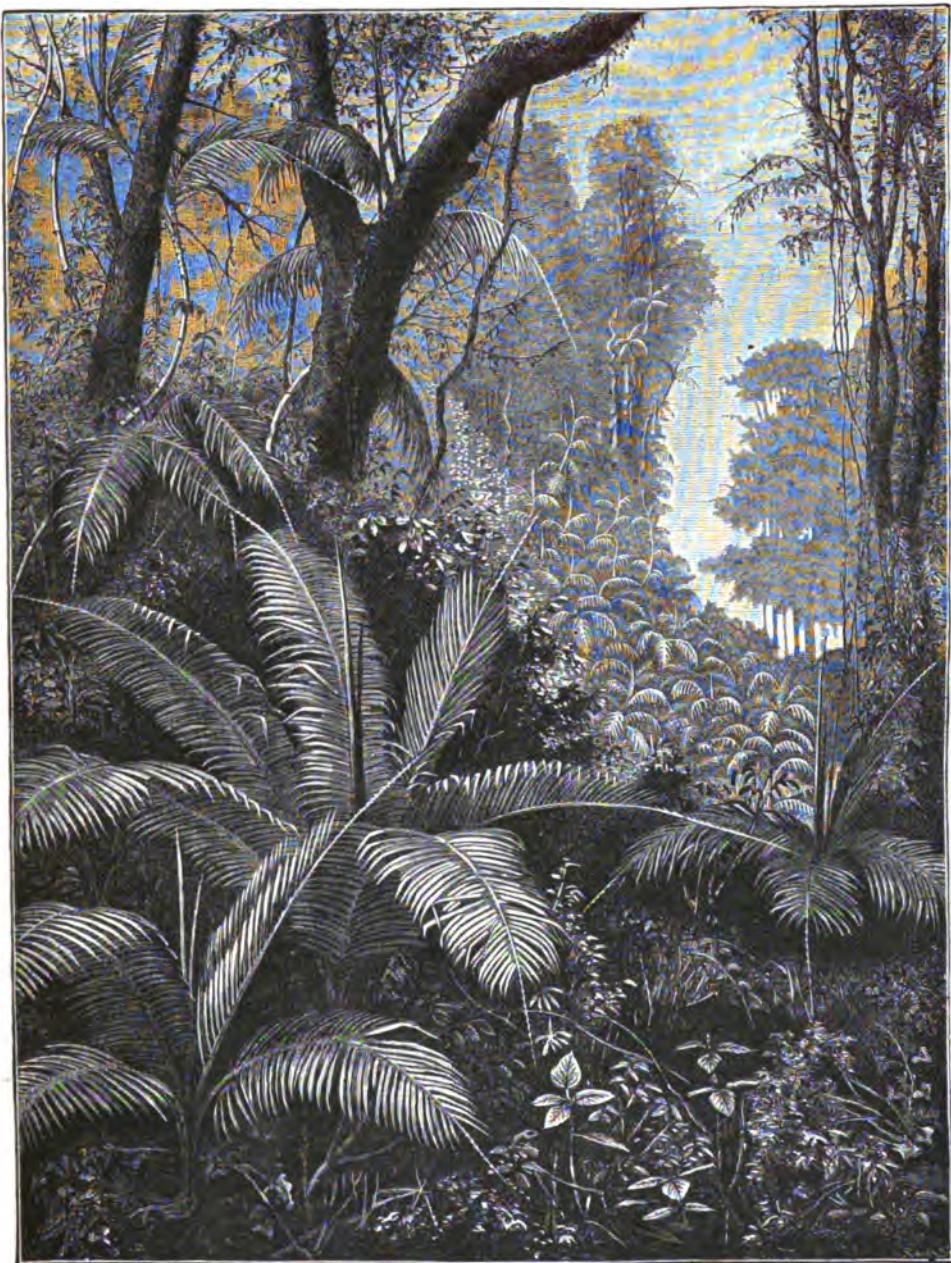


Fig. 94.—Indian Climbing Palms (*Rotang*). From a photograph.

What has been stated here with especial regard to the Rotang or Climbing Palm applies also to all other twining and climbing plants known by the name of *lianes*, and their sap-conducting tubes are the wider, the longer their stems and the larger

their transpiring leaves. In very many lianes the cavities of the conducting vessels can be plainly seen with the naked eye. This is the case, for example, in the cross-section of the liane represented in natural size in fig. 95<sup>6</sup>. A diameter of  $\frac{1}{2}$  mm. is

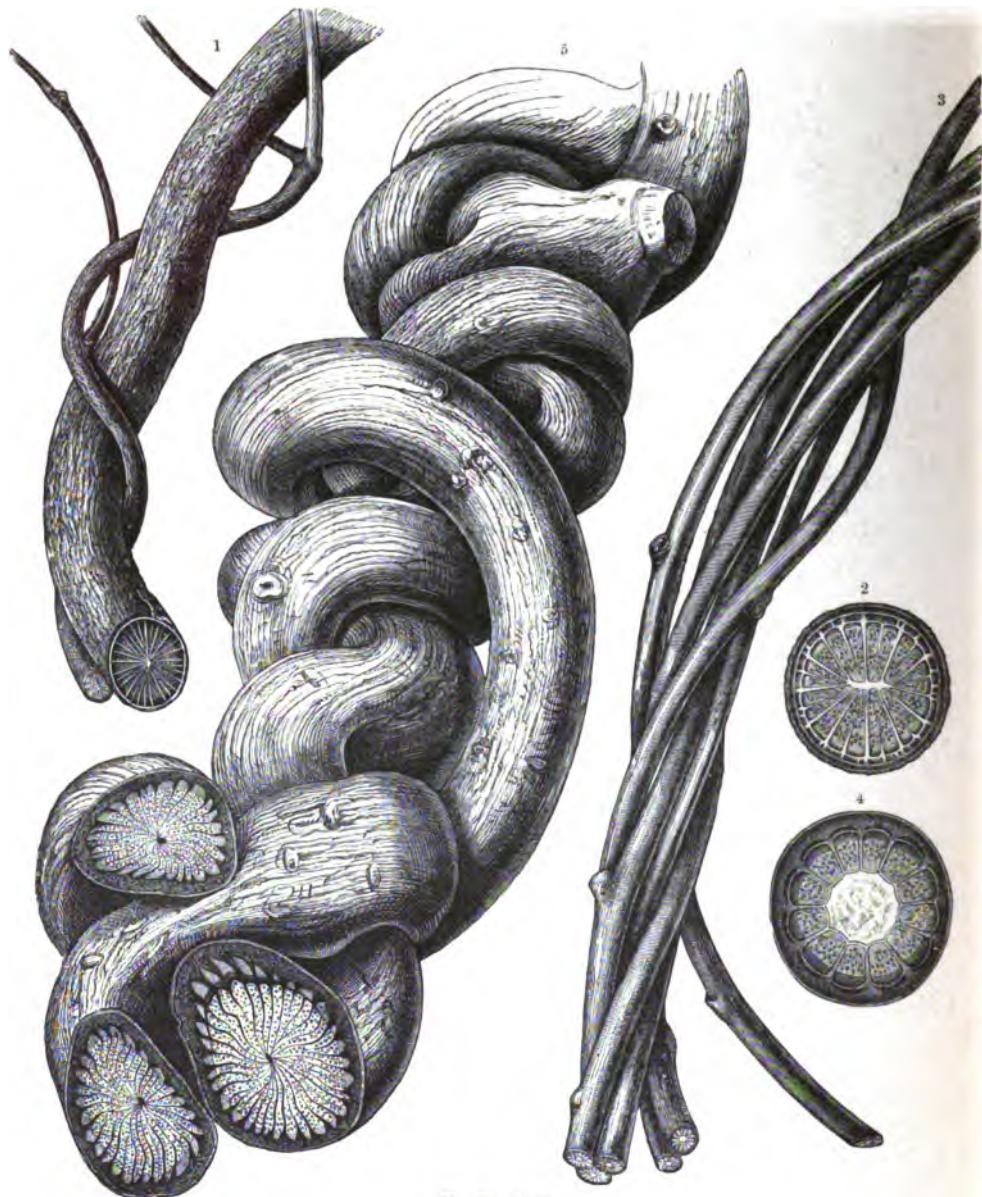


Fig. 95.—Lianæ.

<sup>1</sup> Portion of the stem of a tropical *Aristolochia*. <sup>2</sup> Cross section of a liane-like *Aristolochia*. <sup>3</sup> *Menispermum Carolinianum*. <sup>4</sup> Cross section of the twining stem of *Menispermum* (magnified). <sup>5</sup> Portion of a liane (probably an *Asclepiad*) gathered in a tropical forest; nat. size.

not at all rare in passion-flowers and aristolochias, and, generally speaking, in most twining and climbing plants; whilst in many lianes the conducting tubes have even been observed to be 0'7 mm. in diameter.

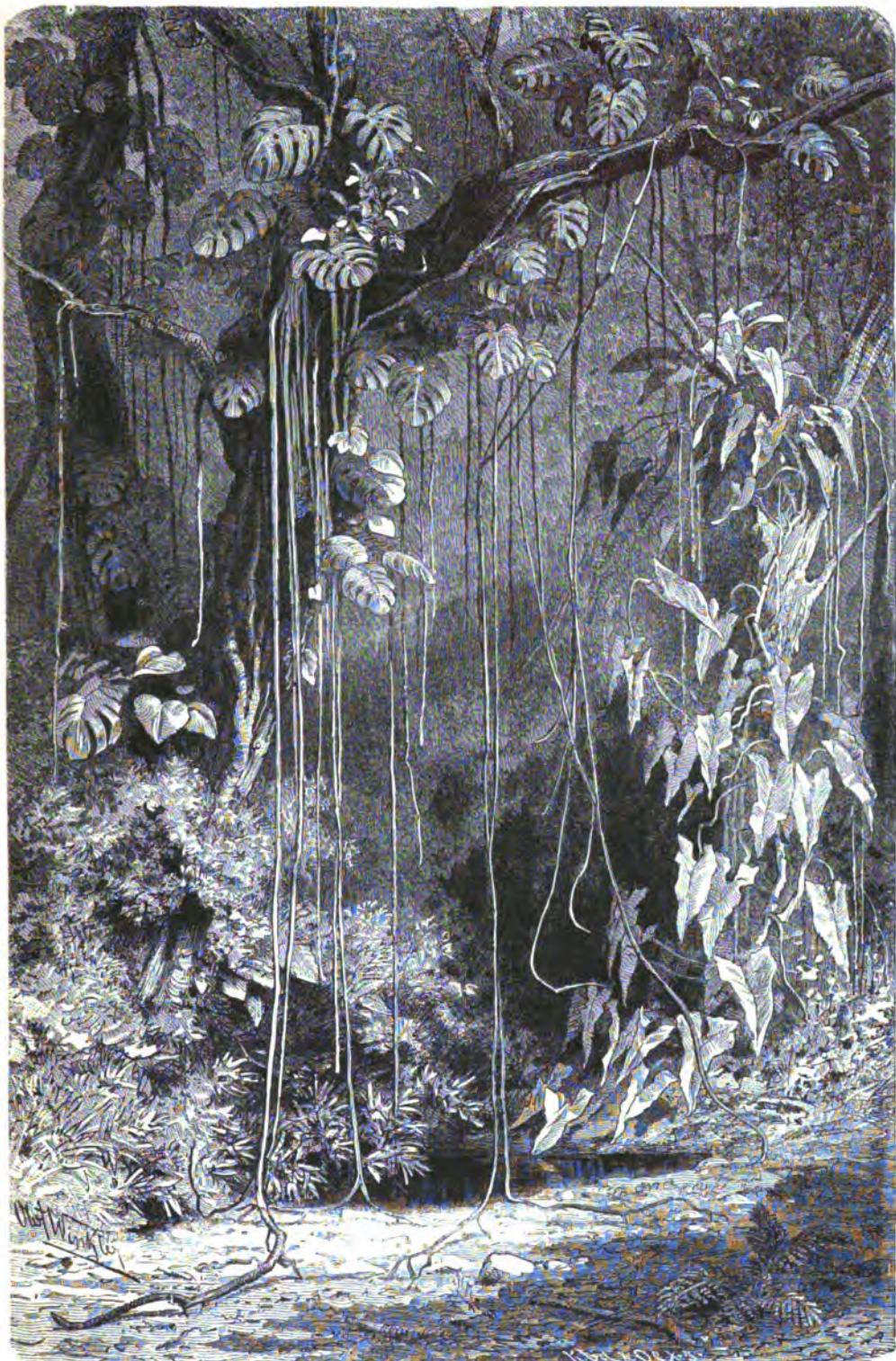


Fig. 96.—Aroids (*Philodendron pertusum* and *Philodendron Imbe*) with cord-like aerial roots.

A particularly noticeable method of conducting water from the soil to the green leaf-blades is exhibited by some large-leaved *tropical Aroids* which climb up trees, and are provided with aerial roots. These plants have really two kinds of aerial roots, viz.: shorter ones, which are at right angles to the stem, by means of which they climb up their support, usually old tree-trunks; and longer ones, passing down perpendicularly to the ground like ropes or strings. In the Mexican *Tornelia fragrans* (*Philodendron pertusum*) represented in fig. 96, these latter roots attain a length of 4–6 metres and a diameter of 1–2 cm. They are of uniform thickness, brown, smooth, unbranched, and quite straight. As soon as they reach the ground, the tip bends round almost at a right angle, and sends a number of lateral roots which are covered with an actual fur of root-hairs into the soil. The bent end then enters the soil for a short distance, and thus the entire aerial root is rendered fairly tense. As a rule, two such cord-like aerial roots originate below each new leaf, and it seems as if this arrangement was specially adapted to transport the necessary food-sap from the soil to the large luxuriant leaf above by the shortest path. But it not only seems so, for this is actually the case, and it is especially remarkable that root-pressure takes a prominent part in the transport. On cutting through one of these cord-like aerial roots about a span above the ground, watery fluid is immediately seen to ooze from the middle of the cut surface. The woody portion of the root, which here forms a central strand, contains very wide conducting tubes, like those in the stems of lianes, and the quantity of fluid exuded in thirty-six hours amounts to as much as 17 grms. It is noteworthy that the root-pressure here, according to all appearances, acts with the same force all through the year. In the vine this is not the case. Vines which are cut through in the summer, it is well known, no longer weep; the cord-like aerial roots of tropical aroids, on the other hand, weep at all seasons of the year when cut across. Indeed, the vegetative activity is never entirely interrupted in these plants all the year, and it should be remembered, in connection with this fact, that they grow in places where the air and soil are always warm, and where their humidity is only subject to slight variations. It may happen that in damp, warm places transpiration from the leaves ceases for a time entirely, and then it is very necessary that the amount of food-sap should be forced up to the leaves by root-pressure in order that they may be supplied with the food-salts they require. The water, which contained dissolved food-salts, is of no use when it has given these up, and it is therefore forced out of the stomata, these in consequence being transformed into water pores.

The aerial roots, which form the shortest and straightest channels for conducting the raw food-sap to the leaves, are, moreover, of great importance to these tropical aroids, since it not infrequently happens that the lower portion of the stem in an old plant dies off, leaving the upper part, which is fastened to the trunk of a tree by the earlier-mentioned short supporting roots, and therefore in no direct connection with the ground. The supporting roots would not be sufficient to supply the fluid food required, and the whole plant is therefore provided

with this food only through these cord-like aerial roots which are sent down into the soil.

These few examples are enough to show that the construction of the stem and roots stands most intimately related to transpiration, inasmuch as the transpiring green tissue is effected by the structure. But since the construction of these plant members, *i.e.* the architecture of the stem, is also dependent upon various other vital processes to be described later, it would not be fitting to discuss their relations here in detail, and their treatment must be postponed until a later section.

---

## 5. CONDUCTION OF FOOD-GASES TO THE PLACES OF CONSUMPTION.

Transmission of the food-gases in land and water plants and in lithophytes.—Significance of aqueous tissue in the conduction of food-gases.

It has been repeatedly pointed out that a division of labour occurs in all large plants, so that one portion of the cells provides for the reception of water and food-salts, another for that of food-gases, and yet another for the conduction and transmission of fluid and gaseous nourishment to the places where they are consumed.

How the aqueous food-salt solutions derived from the soil are brought to the green tissue, what contrivances are thereby brought into action, and what phenomena of plant-life are related to this conduction have been discussed, as far as practicable, in the previous pages, and it now only remains to describe the transmission of the gaseous food-materials. This is far more simple than the conduction of the solutions of food-salts. The most important of the food-gases in question are *carbonic acid* and *nitric acid*. Carbonic acid is continually being conducted by means of water to the green tissues. The shortest passage is to be found in aquatic plants whose protoplasm, provided with green chlorophyll and in need of carbonic acid, is only separated from the surrounding water by a thin cell-wall, while this water always contains carbonic acid, though perhaps only in small quantity. Under the influence of sunlight, the groups of green cells in hydrophytes form a centre of attraction to the carbonic acid, which is sucked up with great energy from the surrounding water, passes easily through the cell-wall, and so comes directly into the neighbourhood of the green protoplasm, *i.e.* that place where its decomposition is effected. The green cells of water plants therefore furnish an apparatus for both absorbing and decomposing carbonic acid, and usually no further means and no special conduction through other cells are required.

In *lithophytes* it is otherwise. Here we have the remarkable fact that they are only active at times; only, that is to say, when they are sufficiently moistened by rain, dew, and mist, and are to some extent submerged for a time by heavy down-pours. In dry air their vital activity is suspended; they then adhere to the rocks like

withered turf and dry scales, as if dead. But as soon as they are moistened, or can condense moisture from the air, they are aroused to renewed vitality, and then suck up with great eagerness atmospheric water, which always contains small quantities of carbonic acid gas, and also traces of nitric acid. In the rock-inhabiting mosses the cells, which absorb water from the atmosphere containing carbonic acid, are also those in which the decomposition of carbonic acid takes place. In this respect these mosses behave exactly like aquatic plants; nor is it perhaps superfluous here again to point out the interesting fact already mentioned, that there are mosses which permanently live under water, and there behave like true water plants, though they are able equally to live on rocks, where they remain dried up for weeks together, and only resume their activity when wetted by rain. It is to be taken for granted that such damp, water-saturated mosses have the capacity of absorbing carbon dioxide from the surrounding atmosphere. The carbon dioxide is changed into carbonic acid by its passage through the cell-wall saturated with water. Probably it is only when carbonic acid is dissolved in water that it reaches the active protoplasm in the cells in question. In lichens the carbonic acid which reaches the protoplasm provided with chlorophyll is also dissolved in water; however, in most lichens the green cells do not come in contact with the atmosphere, but are separated from it by a layer of hyphal threads. Thus the conduction to the green cells takes place by means of the hyphal layer destitute of chlorophyll.

In land plants also the cells which are filled with chlorophyll-bearing protoplasm seldom come directly into contact with the atmosphere; usually the green tissue is surrounded with an actual mantle of water. That is to say, the cavity of each epidermal cell contains very watery fluid, or, in other words, in the fully-formed epidermal cells the protoplasm constitutes merely the parietal layers without chlorophyll, their large cavities being filled with water. These epidermal cells fit closely to each other, and on the upper side of the leaf are only rarely interrupted by stomata. Usually the epidermis on the upper side of the leaf gives rise to a layer of cells with clear watery contents, directly bordering on the green palisade tissue; and as the carbon dioxide of the atmosphere has to pass from the upper side to this green tissue, it must first of all pass through this watery cell-layer of the epidermis. There it becomes changed into carbonic acid, and passes from this epidermal sphere of activity, not in the form of gas, but dissolved in water, to the cells of the palisade tissue below. Since the green palisade tissue under the influence of sunlight uses up the carbonic acid in the manufacture of organic material, it becomes a centre of attraction for this acid as long as the illumination continues. At first the carbonic-acid-bearing contents of the contiguous cells are eagerly absorbed, and indirectly carbon dioxide also is drawn from the surrounding air and made to force its way into the epidermal cells. The cell-wall offers no great resistance to this entrance. It has been proved that carbonic acid, or rather carbon dioxide, passes very easily through the cell-wall. According to all this, it is evident that the small quantity of carbon dioxide is drawn from the air by the green illuminated tissue of the leaves and stem, that carbon dioxide streams

rapidly towards these parts, penetrates into the epidermal cells, is changed into carbonic acid, and reaches the green tissue by means of the aqueous contents of the epidermal cells.

According to the previous statement, which has been discussed in detail, the epidermis has also to provide for the transmission of the carbonic acid to the places of consumption, viz. to the green tissue.

In accordance with climatic and other local conditions, and corresponding to the individuality of separate species, the epidermis presents, as is well known, endless variations in structure. This variety of formation is concerned chiefly with the part which it has to play as a protective covering, as strengthener, and the like. As a conducting apparatus for carbonic acid, that is, in the form of a water mantle or outer aqueous tissue, it exhibits comparatively little variation. In evergreen plants which grow in warm, damp situations where transpiration is limited, and where the water of the soil is often conducted by root-pressure to the large transpiring leaf-surfaces, as, for examples, in tropical bananas, palms, mangroves, figs, and peppers, the aqueous cells which lie above the green palisade tissue are always arranged in several layers. In all those plants also whose outermost cells in contact with the air have much thickened walls, and consequently a restricted lumen, as, for example, in the Oleander, which grows on the sides of brooks (see fig. 73<sup>3</sup>), and in the proteaceous *Dryandra floribunda* growing in the Australian bush (see fig. 68), the water mantle consists of a double layer of cells. When the green tissue is penetrated by vascular bundles and groups of strengthening cells without chlorophyll, the aqueous epidermal layer is also interrupted, and is usually only co-extensive with the palisade cells. In the leaves of grasses the colourless aqueous cells form rows which are placed above the green assimilating tissue, and surround this tissue as an actual mantle.

The demand of the green tissue for carbonic acid regulates itself to the consumption in the formation of organic substances. But the consumption is at a maximum at the time of strongest illumination and greatest warming of the green tissue, and therefore coincides with the most abundant transpiration. At such a time the carbonic-acid-bearing sap is drawn by the active protoplasm in the green tissue with great eagerness from the epidermal cells lying above, often so abundantly that a quick replacement is impossible. But in consequence of this the epidermal cells lose their turgescence; they collapse, and the hitherto tense epidermis presents a flaccid appearance. In order that this collapse may take place without injury, the following contrivance has been devised. The side-walls of those cells which form the epidermis, i.e. the outer aqueous tissue, are delicate, thin, and flexible, and as these cells give up a portion of their sap, their side-walls are folded together just like a bellows from which the air has been expelled. When the cells become again filled with fluid, the folds are straightened out as in a bellows filled with air, and the cells regain their former tenseness.

In the course of the foregoing representation we have only described the transmission of carbonic acid through the epidermal cells rich in watery cell-sap on

the upper side of the leaf. But it must not be forgotten that the same process also takes place on the under side of the leaf, particularly when the green tissue is not divided into palisade cells and spongy parenchyma, and also when the epidermis is provided with stomata both on the upper and under sides of the leaf. In certainly 70 per cent of all leafy plants the arrangement is such that palisade tissue occurs beneath the succulent epidermis of the upper side, under this again spongy parenchyma, and again under this the epidermis of the lower side, which is abundantly pierced by stomata. It can therefore be asserted, for the majority of plants with green foliage, that the epidermis of the upper side chiefly regulates the transmission of carbonic acid to the palisade cells, and that transpiration is chiefly regulated by the epidermis of the lower side.

It is hardly probable that carbonic acid finds entrance to the green tissue through the stomata. At the time when the demand for carbonic acid is at a maximum in the green tissue, a considerable quantity of food-salts must be delivered to the green cells, and the water which provides for the transport of the food-salts from the soil up to the small chemical laboratories, as the palisade cells may be called, is rapidly expelled from the stomata in the form of vapour. But while water-vapour is streaming out of the stomata, the carbon dioxide of the air can hardly stream in through the same avenues at the same time, and it may be concluded that when, generally speaking, this gas is absorbed through the stomata, the occurrence is exceptional.

Concerning the filling of the epidermal cells with water and carbonic acid, it should be here again pointed out that in not a few plants the absorption of rain and dew takes place directly through the foliage-leaves. Since rain and dew always contain small quantities of carbonic acid and traces of nitric acid, this method of filling the epidermal cells is so much the less to be undervalued. In very many green foliage-leaves the continuous epidermis above the palisade cells is capable of being moistened, while the lower epidermis, rich in stomata, on the other hand, is kept dry by the most varied contrivances; and it is very probable that in such cases the water of rain and dew is taken up by the whole epidermis of the upper leaf-surface, especially when these epidermal cells have a short time previously given up a portion of their contents to the green tissue, and have become consequently somewhat collapsed. In many cases it must be concluded, from their shape and position, that the filling of the epidermal cells is only caused by the watery sap brought from the roots, and indeed only by means of the green palisade tissue, i.e. of the same tissue which, on occasion, again receives watery fluid from the epidermal cells. This periodic alternation of absorption and expulsion may be explained in the following manner. The water arriving from the soil is given off by the palisade tissue to the epidermal cells at certain times, i.e. when no carbonic acid is required, in order that carbon dioxide may there be drawn from the air and changed into carbonic acid. When this has happened, and a demand for carbonic acid is set up in the palisade tissue, this tissue takes back the water it had previously given off, now of course accompanied by the absorbed carbonic acid.

# FORMATION OF ORGANIC MATTER FROM THE ABSORBED INORGANIC FOOD.

---

## 1. CHLOROPHYLL AND CHLOROPHYLL-GRANULES.

*Chlorophyll-granules and the sun's rays.—Chlorophyll-granules and the green tissue under the influence of various degrees of illumination.*

### CHLOROPHYLL-GRANULES AND THE SUN'S RAYS.

In the former section of this book it has been described how everything which serves as food for plants is conducted to the green tissues. Food-salts, food-gases, and water arrive at the same goal by the most diverse contrivances—to the green cells as those places where the raw material is worked up and organic substances prepared from it; to the place of need where the materials for further building and development, for rejuvenescence, multiplication, and reproduction of the plants in question have to be provided. The question how living plants manufacture organic substances in the green cells from the raw materials which stream to them, particularly from the raw food-sap and carbonic acid, must now be discussed.

First, it should be remembered that the formation of organic materials always commences with the decomposition of the absorbed carbonic acid. This decomposition, however, is only carried on by that protoplasm in which are imbedded *chlorophyll-granules*. The protoplasm in question can only accomplish the indicated task by the help of these structures, and the chlorophyll-granules are therefore really the organs on which everything depends. It is in them that those remarkable processes are carried on, upon which depends the renewal, and ultimately the existence, of all life. The description of these organs must, therefore, precede all further discussion.

Having regard to the importance of their function, the structure of the chlorophyll-granules appears to be simple enough. It is possible that later researches, with instruments and methods of observation more perfect than those now at our disposal, will furnish more accurate details about their minute structure, and particularly as to their dissimilarity from the protoplasm in which they are imbedded. In the meantime, only this much is known—that the ground-work of the chlorophyll-granules differs but little in its structure and composition from the surrounding protoplasm. Like all sharply-defined protoplasmic bodies, chlorophyll-granules exhibit a pellicle-like thickened outer layer; the inner portion, on the

other hand, is formed of a porous mass of reticular or scaffold-like strands, which may best be compared to a bath sponge. The holes and meshes of this spongy colourless ground substance contains a green colouring matter, which is dissolved in an oily material, and clothes the continuous small spaces in the form of a parietal layer. This green colouring matter of the chlorophyll-granules, which has been called *chlorophyll*, is easily soluble in alcohol, ether, and chloroform. If green leaves are steeped in an alcoholic solution, they become blanched in a short time, and the colouring matter passes entirely into the fluid. The alcohol assumes the beautiful green colour which the leaves formerly possessed, and the previously green leaves are now to be seen floating in the green alcohol. In transmitted light the solution appears a beautiful green; but when observed in reflected light it appears blood-red, and therefore the colouring matter displays a marked *fluorescence*. If a fatty oil is added to the green-tinted alcohol, and the two are shaken up together, the green colour passes into the added medium, while in the alcohol a yellow substance remains, which has been termed *xanthophyll*. The chemical composition of chlorophyll is not yet so clearly understood as we could wish. It is asserted that it is possible to obtain chlorophyll in a crystallized form. The crystals obtained form green transparent rhomboids, which, when exposed to the light, slowly decompose again. This chlorophyll behaves like a weak acid; contrary to earlier belief, it is free from iron, but leaves behind almost 2 per cent of ash, consisting of alkalies, magnesia, some calcium, phosphoric and sulphuric acids. The fact that the production of these crystals must be preceded by a series of long-continued operations, together with the fact that chlorophyll is extremely delicate and easily decomposed, always allows us to suppose that the crystals mentioned are only a product of decomposition, and do not belong to that chlorophyll which colours the chlorophyll-granules in living cells. It was previously thought that chlorophyll was a mixture of two colouring matters, viz. a blue and a yellow, until later researches demonstrated that this supposition was unfounded, and that a false impression had been received through observation of the process of decomposition. A characteristic absorption spectrum has been obtained for chlorophyll, which is especially useful in all cases where it is a question of demonstrating the presence of very small quantities of the colouring matter in any parts of the plant. With respect to this it is enough to say that the whole of the violet and blue and the ultra-violet rays are cut off from the spectrum, and that it exhibits seven characteristically distributed absorption-bands. It may be further remarked here that after treating the chlorophyll with hydrochloric acid tiny crystals arise, which have been called *hypochlorin*. The results of all these researches have thrown but little light upon the part which chlorophyll plays in those processes which commence with the decomposition of the absorbed carbonic acid in the chlorophyll-granules.

Compared with the size of the whole mass, chlorophyll forms only an extremely small fraction of the granules it colours green, and when it is withdrawn by the addition of alcohol, only the colour and not the size of the granules in question is found to be altered.

Chlorophyll-granules appear to be imbedded in protoplasm from their origin until their disappearance. When the protoplasm is situated round the wall—or, in other words, when the central cavity of the protoplasm is large and filled with watery cell-sap, and the plasma which surrounds the sap-cavity is sac-like and only forms a thin covering to the cell chamber, then the chlorophyll-granules are usually imbedded in the middle layer of the parietal plasma, so that they are separated from the sap-filled central cavity, as also from the cell-wall, by a layer of colourless protoplasm. The same thing occurs when the chlorophyll-granules are imbedded in the plasma strands which are stretched across the cell-cavity (see figs. 5<sup>2</sup> and 5<sup>3</sup>). Frequently the chlorophyll-granules project like warts, and thus give a knotty appearance to the protoplasmic strands; but even then they are always covered by a thin colourless layer of protoplasm.

In spite of this close connection, chlorophyll-granules always appear to be sharply defined, and exhibit in their entire development a certain separateness from the protoplasm in which they may reasonably be supposed to take their origin. They enlarge, divide, and multiply, and occasionally in the course of their life alter their form. With respect to their shape there is little variety in the green tissue of the stem and leaves of higher plants. The chlorophyll-granules almost always appear there as rounded or occasionally angular, sometimes even as lenticular or many-sided grains. A much greater diversity is observed in those simple green plants which live in water, and have been classed together under the name of Algae. In the cells of the green filaments of *Zygnema*, which are represented in fig. *m* of Plate I., the chlorophyll bodies are stellate, and are so arranged in each cell that there are usually two stars side by side. In species of the genus *Spirogyra* (Plate I., fig. *l*) they form spirally wound, usually knotty, bands, and in most species of the genus only one band in each cell; but in some species there are two bands, whose spirals cross one another, whereby very ornamental structures come into view under the microscope. In species of the unicellular *Penium* (Plate I., fig. *k*), the chlorophyll bodies form plates or bands parallel to the long axis of the cell, projecting against the cell-wall in all directions. In *Mesocarpus* a single green plate is observable, which divides the cavity of the cell into two almost similar halves; *Edogonium* exhibits a latticed plate; species of the genus *Ulva* have plate-shaped chlorophyll bodies which lie close to the wall; in the cells of *Podosira* are seen disc-shaped chlorophyll bodies which jut out in all directions; and in the liverwort *Anthoceros* the chlorophyll bodies are in the form of hollow spheres surrounding the centres of the cells.

The number of chlorophyll-granules in the protoplasm of the cell varies from one to several hundreds. In the cells of selaginellas there are usually 2–4; in those of the luminous moss, *Schistostega osmundacea*, to be described later more in detail, 4–12 (Plate I., fig. *p*). The green cells of most leafy flowering plants contain 20–100, many even 200. In the cells of *Vaucheria* (Plate I., fig. *a–d*), the protoplasm is so crowded with thickly-pressed small green granules as to make one think that the whole cell-body contained but a single chlorophyll mass. Foliage-

leaves, in which a distinct separation between the palisade and spongy parenchyma is completed, always show many more chlorophyll-granules in the former than in the latter. Careful countings have shown that the palisade cells usually contain three or four times—occasionally even six times—as many chlorophyll-granules as the adjoining cells of the spongy parenchyma. When the chlorophyll-granules in a cell are so many that the whole inner wall of the cell can be covered with them, they arrange and distribute themselves very equally in this manner, and such cells appear uniformly green. It then seems as if the whole cell-chamber were entirely filled with chlorophyll-granules, but this is not really the case. The central cavity of the protoplasm filled with cell-sap never contains a single chlorophyll body.

The chlorophyll-granules imbedded in the parietal protoplasm can also undergo the most remarkable displacements, which we will forthwith describe.

With regard to shape, cells with active protoplasm, containing chlorophyll-granules, exhibit the widest variety. Especially are all imaginable cell shapes to be found in the group of Desmids which live in water: rod-shaped, cylindrical (Plate I., fig. *k*), crescent-shaped (Plate I., fig. *i*), tabular, stellate, tetrahedral, and many others for which it would be hard to find short and suitable names. The Algae, which to the naked eye seem composed of green threads, are built up of cells which are, for the most part, tubular and cylindrical (Plate I., figs. *a*, *b*, and *l*, *m*). In Lichens and Nostocaceæ the cells which form the tissues are spherical; in Mosses and Liverworts they are pentagonal and hexagonal.

As already mentioned in former sections, the green tissue in the foliage of Phanerogams is formed, in the majority of instances, of two kinds of cells—of branched cells forming the spongy parenchyma, and of cylindrical cells which constitute the palisade tissue (Plate I., fig. *r*). The latter are often short, their length being not much greater than their width, but usually they are five or six times, and occasionally even ten or twelve times, longer than broad. In bulbous plants the palisade-shaped cells are arranged parallel to the upper leaf-surface, but in the majority of seed-bearing plants they are at right angles to the upper surface of the foliage-leaf, as shown in the cross-section of a leaf of the Passion-flower in Plate I., fig. *r*. The green cells below the epidermis of pines and various firs exhibit a very peculiar form. In contour they appear angular and tabular, and are fitted closely to one another without intercellular spaces. From the cell-walls parallel to the upper surface of the leaf trabeculae project into the interior, by means of which each cell is divided up into niches usually of equal size. Such cells remind one of stables in which the stalls of the different horses are separated by boarded partitions. The projecting trabeculae are always so arranged that the entire cell-chamber appears like a group of palisade cells whose side walls separating one from another have been interrupted. These partitions, which, as stated, are to be found in many firs, but also in grasses and many Ranunculaceæ—especially in the Monkshood (*Aconitum*), Peony (*Paeonia*), and Marsh Marigold (*Caltha*)—increase the internal surface of the chamber, and this appears to be advantageous, inasmuch as by this means many more parietal chlorophyll-granules can find a place than would

be possible in a single cell of equal dimensions, but devoid of such projecting trabeculae.

It is shown by very accurate investigations that the quantity of organic substances formed in a cell, by the decomposition of carbonic acid, is greater the greater the number of chlorophyll-granules, provided that all of them are so arranged within its protoplasm that they can discharge their functions. A heap of chlorophyll-granules filling the cell irregularly would be little suited to effect this result. The small, green chlorophyll-granules must, on the contrary, be so arranged that no one deprives another of light, and this is most easily possible, especially in a many-storied plant-structure, composed of numerous cells, when the chlorophyll-granules are grouped together like the stones in a mosaic, and are arranged along the walls in this order. When, moreover, the light falls unhindered through certain portions of wall, as through a window into the cell-cavity, all the chlorophyll-granules there situated are almost equally illuminated. The larger the extent of wall surface, the more chlorophyll-granules can be accommodated on it, and therefore the more abundantly can the decomposition of carbonic acid be carried on in such cells. For such green multicellular tissue, whose most important function is the decomposition of carbonic acid and the formation of organic substances, the parietal grouping of the chlorophyll-granules, the above-mentioned infolding of the inner surface of the cells, generally the increase of the inner surface of the cell-walls clothed with chlorophyll, is accordingly the most advantageous arrangement for the best possible utilization of the available space.

When one speaks of the "green" of plants one thinks first of all of the foliage-leaves, in which that colour is especially noticeable. The name "chlorophyll" translated by "leaf-green" might lead to the idea that cells and tissues provided with chlorophyll are only to be found in the leaves; but this would not at all correspond to the true state of the case. Those plants which are not differentiated into stem and leaves, especially the many kinds of green water-plants classed under the name of *Algæ*, generally consist entirely of chlorophyll-bearing cells. In those mutually-nourishing combinations named Lichens, one of the partners is without, while the other is provided with, chlorophyll.

When stem and foliage-leaves are clearly differentiated, a portion of the tissue is deprived of chlorophyll while the other portion is more or less rich in the same. Chlorophyll-containing tissue is found in all the members of these stem-plants, in roots, in stems, in foliage, in floral leaves, in fruits, and seeds. In tropical orchids the aërial roots when dry appear white and are seemingly quite devoid of chlorophyll; but when moistened their green colour is seen, because when the outer porous covering is filled with water, and its cells become transparent, the colour of the green tissue-layer below shines through. There are even orchids, e.g. *Angræcum globulosum*, *funale*, and *Sallei*, which, when not flowering, have no other green tissue than that in the aërial roots, and in which not only the absorption of food-materials, but also the working up of the absorbed nourishment, particularly the decomposition of carbonic acid and the formation of organic substances, is carried

on by the green tissue of the aërial roots. Green tissue is much more frequently to be met with in stem-structures than in roots. Hundreds of rushes, bulrushes, cyperuses, and horse-tails, as well the Casuarinææ and species of *Ephedra*, included under the switch plants, many papilionaceous plants of the genera *Retama*, *Genista*, and *Spartium*, a number of *Salicornias*, tropical orchids, and cactiform plants, the Duckweed (*Lemna*), and all the plants possessing flattened shoots (see fig. 82), contain green tissue, without exception, in the cortex of their stem and branches. Also ovaries and fruits which are not yet fully ripe are so universally coloured green that in popular language green fruit and unripe fruit are synonymous. Chlorophyll is more rarely observed in seeds. Those whose embryos are differentiated into axis and leaf only seldom—as, for example, in the pines—show green tissue in the cotyledons. The seeds of orchids, especially those living epiphytically on the bark of trees, behave in a peculiar manner. These are marvellously small, consist of only a single group of parenchymatous cells, and no trace is to be seen in them of a radicle or cotyledon. They only retain the capacity of germinating a short time, and it is important to these seeds, which are poorly supplied with reserve food, that immediately after leaving the fruit-capsule they may be able to provide themselves with nourishment from their surroundings, and to manufacture organic substances from this food. This they can naturally only do by the help of chlorophyll, and it is interesting to notice that they also are actually endowed with this substance. Even when they are still inclosed in the capsule of the parent plant these seeds become green, and when they are carried by the wind into some cleft on the bark of an old tree-trunk the chlorophyll is able at once to function. After a short time a small green tubercle grows out of the green seed, and fixes itself by absorbent cells to the substratum, then very gradually it grows up to form a large plant-stem.

Large flowers whose petals, from the commencement to the end of the flowering period, exhibit a green colour are esteemed rarities. On the other hand, small floral leaves, rich in chlorophyll, are of very common occurrence. The change of the floral colour also, during the flowering period, from white, red, violet, and brown, to green, has been frequently observed in small as well as in fairly large flowers. A very striking example of this is the Black Hellebore (*Helleborus niger*). When its flowers open, the outer large leaves situated below the petals (which are transformed into small nectaries), are snow-white, and show up conspicuously from their darker surroundings. From afar they attract the attention of honey-collecting insects, by whom they are eagerly sought out. When, by means of these honey-sucking insects, pollination is brought about, the small nectaries, as well as the large dazzling-white outer floral leaves called sepals, become superfluous. The nectaries forthwith fall off, but the large sepals remain and take up another function. Chlorophyll is abundantly developed in their cells; the white colour disappears; fresh green appears in its stead, and the same floral leaves which previously had attracted insects by their conspicuous colour now function as green leaves exactly like foliage-leaves. A similar alteration of colour, which also has the same

significance, is observed in many orchids and liliaceous plants, but on the whole such a change of function in floral leaves is not common. These cursory observations must show that chlorophyll may appear in all the members of a plant, although it is also true that foliage-leaves chiefly contain the green tissue, so that certainly in 90 per cent of all chlorophyll-bearing plants the decomposition of carbonic acid is carried on in the foliage-leaves.

If, now, after the description of the arrangement, form, and distribution of chlorophyll-granules, we would also learn something as to how organic substances are formed in the cell-chambers by means of these structures, we find ourselves in the position of an inquirer who visits a chemical laboratory without a guide, and wishes to ascertain in what way some material—for example, a pigment—is manufactured. He notices apparatus set up there, sees the raw materials heaped together, and also finds the finished product. If the manufacture is actually proceeding, he can also observe whether warmth or cold and greater or less pressure are brought into action as propelling forces, and he can, if intrusted with the manipulation necessary to the production of such pigment, imagine the relation of the different parts to the whole. Of the details, indeed, much must remain incomprehensible, or quite unknown. Especially with reference to the quantity of the transformed raw material, and with regard to the propelling forces, must the visitor's knowledge remain incomplete.

It is not otherwise with us when we would inspect the processes carried on in the cells where chlorophyll-granules develop their activity. We see the effective apparatus, we recognize the food-gases and food-salts collected for working up, we know that the sun's rays act as the motive force, and we also identify the products which appear completed in the chlorophyll-granules. By careful comparison of various cells containing chlorophyll, on the ground of observations which establish the conditions under which the manufacture of organic substances succeeds best and worst, having found by experience that under certain external conditions the whole apparatus becomes disintegrated and destroyed; it is indeed permissible to hazard a conclusion about the character of the propelling forces. But what is altogether puzzling is how the active forces work, how the sun's rays are able to bring it about that the atoms of the raw material abandon their previous grouping, become displaced, intermix one with another, and shortly appear in stable combinations under a wholly different arrangement. It is the more difficult to gain a clear idea of these processes, because it is not a question of that displacement of the atoms called decomposition, but of that process which is known as combination or *synthesis*. Decompositions and analyses, even of the most complicated compounds into simple combinations are well understood, but not so the converse. It is always considered a fortunate occurrence when a chemist succeeds in producing from its fundamental elements, or from the simplest combination of these, one of those complicated bodies, which are, nevertheless, formed with such ease in plant cells. When sugar is "made" in a manufactory, it is not that carbon and the elements of water are used, although these are so abundantly

at disposal, but only that the sugar is isolated which has been formed synthetically from these substances in those tiny chemical laboratories, the vegetable cells. Consequently it is really incorrect to say that sugar is "made" in our manufacturers; we should only say that there the sugar manufactured by the plants is separated from other substances and prepared for further use.

Although it is not possible to represent the processes concerned in the synthesis of organic materials in plant cells as a matter beyond all doubt, one is justified in taking refuge in hypotheses. And it must be looked upon as an hypothesis when we consider the movement by which the atoms of the food-gases and food-salts are displaced by the sun's rays in the vegetable cells as a transmission of the vital force of the sun. The atoms have arranged themselves by this movement in a different order, they hold and support one another, they are stable, and a condition of mutual tension has been set up. The vital force of the sun has become the hidden spring of all these changes. The now stable organic material formed by synthesis is thus equipped with an adequate supply of energy, designated in other words as latent heat. If the atoms of the organic material from whatever cause again break loose, abandoning their combination and arrangement, they perhaps so displace and rearrange themselves that those groups which previously existed are formed again, and thus the potential energy is changed to vital force, the latent heat to sensible warmth. When a tree-trunk is consumed, the vital force of the sun, which had been changed by the formation of cellulose and the other organic materials composing the wood of that time into latent force, is again transformed into active energy; and when we burn coals, the sun's rays, which thousands of years ago brought about the formation of organic vegetable substances and were imprisoned in the coal, will again be set free, will warm our rooms, drive our machines, or propel our steamships and locomotives. Keeping this idea in view, it is at least possible to imagine the mechanical significance of the sun's rays in the formation of organic substances in plants, and it may be reckoned that the quantity of organic substance produced stands in a fixed proportion (which may be expressed in figures) to the store of energy in the same.

One circumstance on which particular stress must here be laid is that the various rays of which sunlight is composed, the rays with various wave-lengths and refrangibility, which, some of them at least, appear to our eyes as the different coloured bands in rainbows, play each a very distinct part in the formation of organic materials in plant cells. Under the influence of the blue and violet rays, i.e. of those which are most highly refrangible and have the smallest wave-lengths, the oxidation of the organic materials called *carbohydrates* is assisted, that is to say, not the formation but the decomposition and transformation of these compounds are favoured. The red, orange, and yellow, i.e. those rays which are less refrangible and have a greater wave-length, behave quite otherwise. These favour the reduction of carbonic acid, assist the formation of carbohydrates from raw materials, and are therefore chiefly concerned in the originating of such organic substances. When a sunbeam passes through a colourless glass prism a

continuous spectrum is produced—violet, dark blue, light blue, green, yellow, orange, and red. If the same sunbeam passes through a transparent but coloured body, which may be either solid or fluid, whole groups of colour absent themselves from the spectrum. Dark bands appear in the corresponding places, and we say that the light in question has been absorbed by the coloured body. Now, if chlorophyll has the property of absorbing those colours of the spectrum which are not advantageous in the formation of organic substances from raw material, the rôle of this chlorophyll cannot be too highly estimated. It must not be overlooked, moreover, that many bodies have the capacity of absorbing light rays of shorter wave-length, and, on the other hand, of giving out rays of greater wave-length. It is precisely those pigments which are distributed in plants, again above all, chlorophyll, which possesses this property called fluorescence; and we must therefore also assign this significance to chlorophyll, that it can transform rays of light which are useless in the synthesis of organic materials into those which show the best possible action in this respect. If the fluorescing pigments of plants (chlorophyll, anthocyanin, phycoérythrin) can transform the violet and blue rays into yellow and red, it is to be supposed that their activity goes further, and that they will be able to change rays of small wave-length and higher refrangibility into rays which are found beyond the red, which are imperceptible to our eyes, and which possess very great heat-giving powers, or, in other words, that they will be able to transform light into heat. From all this it may be seen that the significance of chlorophyll in the formation of organic materials would be three-fold. First, a retention or extinction of those rays which might hinder the formation of those compounds known by the name of carbohydrates; further, the transformation of rays with short wave-length into those of longer wave-length, which, according to experience, most favourably effect the production of sugar and starch; and, finally, the conversion of light into heat, and ultimately into latent heat.

#### CHLOROPHYLL-GRANULES AND THE GREEN TISSUE UNDER THE INFLUENCE OF VARIOUS DEGREES OF ILLUMINATION.

If it is beyond question that organic materials can only be formed from the absorbed carbonic acid in the presence of chlorophyll, it is, on the other hand, equally certain that the sun creates and works through these formative processes by its rays, and thus, as the propelling force, becomes the fountain of all organic life. The sun rises and sets, day follows night, and during the night the process just mentioned, upon which the existence of the living world depends, is interrupted. But even in the daytime also, the strength of the sun is very unequal; it is one thing at mid-day, when the source of light is in the zenith and the rays fall perpendicularly on the earth, and quite another in the evening, as the illuminating orb sinks below the horizon and the last rays spread almost horizontally over the surface. Clearly it is anything but a matter of indifference to the organs possessing a certain

amount of chlorophyll in what manner the sun's rays light upon them, or what quantity of vital force is transmitted to them in a given time. Various species of plants may make very different demands for sunlight, but for each individual species the need of propelling force fluctuates only within very narrow limits, which cannot be exceeded without injury. The greatest possible equality in the supply of propelling force is an indispensable condition of a successful career. In order to meet the inequality in the flow of light on bright and dull days, and also during various parts of the day, it is arranged that the green organs can turn towards the sun, and that according to the hour of the day and the strength of the sun's rays at that particular time, they can take up a definite position, and again alter this position with ease. And, indeed, the green chlorophyll-granules in the interior of the cells also show this capability of accommodating themselves in accordance with the demand for light as well as the entire cells, and, finally, even the green leaves, together with the stems and branches which bear them.

If one would obtain a clear idea of the withdrawal of the chlorophyll-granules from the sunlight, one must remember, first of all, that these green bodies, whatever may be their form, are imbedded in the protoplasm of the cell, and that the protoplasm is mobile and easily capable of displacement—or, in other words, that the protoplasm which contains the green chlorophyll-granules twists and rotates within the cell it inhabits, and can transport the granules hither and thither. Still more. Chlorophyll-granules can be temporarily heaped up and crowded together in definite places; they may again be separated from one another, and distributed equally throughout the whole cell-body. In the tubular cells of *Vaucheria clavata*, represented in figure *a* on Plate I., the protoplasm forms a lining layer on the inner side of the colourless transparent cell-wall, and is so thickly studded with round chlorophyll-granules that the cell appears of a uniform dark green. But this is only the case with light of moderate intensity. When strongly illuminated the chlorophyll-granules move apart from one another, arrange themselves in isolated balls, and in a very short time, in each tubular cell, dark-green spots and zones may be seen corresponding to the crowded granules, and light, irregular bands appearing in those places from which the chlorophyll has been withdrawn. If the intensity of the light diminishes, the green clusters dissolve, and the former equal distribution and colouring is resumed. In another filamentous green alga, which lives in water and belongs to the genus *Mesocarpus*, each of the long cylindrical cells contains a plate-like chlorophyll body, which in weak diffuse light turns itself at right angles to the incident rays. In this position the broad side, i.e. the larger surface of the chlorophyll body, is turned to the sun, and the incident light is in this way utilized to the utmost possible extent. As the plate-like chlorophyll body usually extends right across the cell, under the conditions indicated, the cell appears of a uniform green colour. If the full rays of the sun fall on such *Mesocarpus* cells, the plate-like chlorophyll bodies begin to turn so that the plane of the plate is parallel to the direction of the rays. Now the narrow side, i.e. the smaller surface of the chlorophyll body, is turned to the rays, and only a dark-green

stripe is to be seen. This turning movement of the chlorophyll body is very quickly performed, and can be repeatedly effected by darkening and illuminating the cells of the *Mesocarpus* filament.

In cells, too, which are joined together to form tissues, this displacement and movement of the chlorophyll-granules often appears. It has been noticed for a long time that in the prothallium of ferns, in the leaf-like liverworts, in the leaflets of many mosses, and even in the large, delicate foliage-leaves of flowering plants, the green tissue appears to be coloured a lighter or darker green according to the intensity of the incident light; that under the influence of intense sunlight they become blanched and yellowish-green, but in weak light assume a darker tint. If a strip of black paper be placed on a foliage-leaf, illuminated by the sun, so that only a portion of the leaf-surface is covered by it, and if the paper be removed after a short time, the portion left uncovered and illuminated by the uninterrupted rays of the sun appears light green, while that part on which lay the strip of paper, and from which the sun's rays were withheld, is dark green. Careful investigations have shown that this change of colour is due to displacement of the chlorophyll-granules. In diffuse light the chlorophyll-granules group themselves on those cell-walls on whose surface the light falls perpendicularly, and consequently in the cylindrical palisade cells of the foliage-leaf on the small walls parallel to its upper surface, and it is clear that such cells (and therefore the tissue formed by them) have a dark-green appearance when looked at in the direction of the incident light. As soon as they are illuminated by direct sunlight, the chlorophyll-granules retire from these walls and take up their position on the cell-walls which are parallel to the direction of the incident light. In palisade cells the chlorophyll-granules group themselves by the side of the long lateral walls, while the short walls, which are at right angles to the rays, are colourless and free from chlorophyll. In the branched cells of the spongy parenchyma the chlorophyll-granules, which in diffuse light were equally distributed in the cell, heap themselves together in groups in the branches, while the central portions of the cells become clear and free from chlorophyll. The whole tissue, however, in which this displacement has been completed appears much paler than before, and displays usually a decidedly yellowish-green tint. This change of position of the granules, according to the intensity of illumination, may be particularly well seen in the very simply constructed leaf-like duckweed, especially in *Lemna trisulca*. Three sections of the green tissue of this plant, vertical to the surface, are shown in fig. 97.

With these phenomena is indeed also connected the alteration of shape which is observed under varied illumination in chlorophyll-granules. In the leaflets of *Funaria hygrometrica*, a moss very common on piles of charcoal, damp walls, and rocks, the chlorophyll-granules, which are close to the outer walls of the cells, are flattened out, angular, and comparable to small polygonal tablets, in diffuse light. They are also so arranged that the entire wall covered by them appears an uniform green, and only narrow, colourless lines remain between them. As soon as direct sunlight falls on them they quickly alter their shape, the tablets becoming hemi-

spherical or spherical bodies, which project towards the centre of the cell-cavity. By this means the area of the chlorophyll-granules attached to the cell-wall is contracted, and consequently the green of the leaf-surface in question is diminished. In the leaves of many flowering plants, also, the chlorophyll-granules which are distributed in the palisade-cells along the elongated side-walls appear, in diffuse light, hemispherical or even conical, and project towards the centre of the cells so that they are illuminated to the greatest possible extent by the light rays passing through. Under the influence of direct sunlight they flatten out, become disc-shaped, and withdraw to some extent from the bright rays passing through the centre of the cells. The significance of all these processes, the changes of shape as well as the displacements of the chlorophyll-granules, is evident when it is considered that an over-abundance as well as a deficiency of light would be prejudicial, and that for every species the quantity of the sun's rays absorbed by the chlorophyll-granules is definite. Protoplasm, provided with chlorophyll,

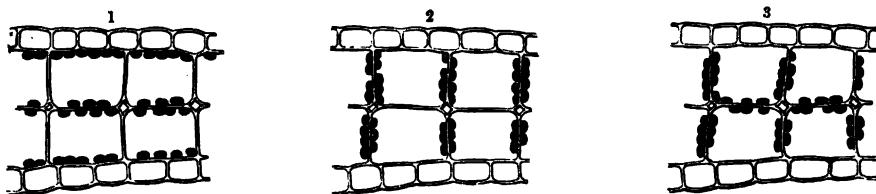


Fig. 97.—Position of the Chlorophyll-granules in the cells of the Ivy-leaved Duckweed (*Lemna trisulca*).

<sup>1</sup> In darkness. <sup>2</sup> In direct sunlight. <sup>3</sup> In diffuse light.

tries under all circumstances to obtain this definite amount. When weakly illuminated, chlorophyll-granules maintain a shape and position in consequence of which they present the largest possible surface to the light; when strongly illuminated, they assume a shape and position by which the smallest possible surface is so exposed. These processes, especially the displacement of the chlorophyll-granules, obtain a heightened interest from the fact that they can only be brought about by the streaming movements of the irritable protoplasm. It must be borne in mind that it is really living protoplasm which displaces the chlorophyll-granules imbedded in it in order to bring them to the places best suited to the illumination then existing, and to place them in sunlight or shade; so that it always happens that the displaced green bodies are neither too much nor too little illuminated.

Many unicellular water-plants, especially zoospores, attain the same result not by displacement of the chlorophyll-granules in the interior, but by movements of the entire cells. These green unicellular organisms may be seen swimming towards the light by means of their cilia, and in this way they take up the position always best adapted to the given conditions. If many swarm-spores are collected together in a limited area, it may happen that they all travel to one particular place; there they swarm about in the water and appear to the naked eye like a little green cloud. Or they may settle on the bottom of the pool, there arranging themselves side by side, so that no one deprives another of light, and they then appear

to the naked eye as green stripes and patches. If swarm-cells of *Sphaerella pluvialis* are cultivated in a flat white china dish filled with rain-water, and one-half of the dish is darkened by means of an opaque body while the other half remains illuminated, the whole of the swarm-cells swim from the darkened to the illuminated water in order to take up a position as favourable as possible with regard to the light. If now the china dish is turned round so that the hitherto illuminated portion becomes darkened and light falls on the part previously obscured, the swarm-cells forsake the position which they had recently taken up, swim from the now darkened place to the illuminated side opposite, and arrange themselves there according as the illuminating conditions are favourable.

If, instead of the *Sphaerella pluvialis* discussed above, clumps of *Vaucheria clavata* are cultivated in a china dish filled with water, and the water is again partially darkened, together with the green tufts growing in it, it will be seen that the cells, which are elongated and fixed at one end, seek with the other end those places where they can find the best light. *Vaucheria clavata*, which has been repeatedly cited as an example, and which is represented in the middle figure on Plate I., consists of long tubular cells, frequently bulging and branched, whose blunt growing ends appear dark green, while the lower dead portions are branched and coloured yellowish-white. The protoplasm is so richly studded with chlorophyll-granules that the entire inner wall of the tubular cells appears covered with a green lining. At the bottom of shallow pools, which is the natural habitat of these plants, they form hemispherical clumps, and all the tubular cells which compose the clumps have their green ends directed upwards towards the source of light. The same thing occurs when the *Vaucheria* cultivated in the china dish is uniformly illumined from above; but, if partially obscured, those filaments over which the darkening shadow is thrown very quickly alter their position. They bend towards the light side, and then the clump looks just as if its filaments had been combed in this direction. Moreover, the same thing is also seen when the china dish containing clumps of *Vaucheria* (on which until now diffused light has fallen uniformly from above) is placed at the further end of a one-windowed room, so that the light can only reach it from one side. Here, again, all the filaments, or rather, tubular cells of the clump, bend towards the source of light, and if they continue to grow, the increase in length is universally in a line with the direction of the incident rays. After a few days these *Vaucheria* clumps also look as if they had been combed out.

The green tissues of thallophytes, and the green leaves and stems of ferns, and phanerogams, i.e. those extensive combinations of green cells whose function is to work in a harmonious manner, and to manufacture organic substances for the plant to which they belong from carbonic acid with the help of other food-materials; these behave in the same way as the individual green cells which swim freely in water, and as the tubular cells of *Vaucheria*, which are attached at one end. Arrangements are necessary for these likewise, by which they can always be placed in the most favourable light. Of course, in these plants where

division of labour has been so far developed, the conditions are not so simple as in those plants which consist only of single cells, and it is naturally to be expected that, according to the character of the individual species and the places which they inhabit, the arrangements would be very varied. The fact must also be kept in mind that each spot on which a plant has settled itself in the course of time may undergo alterations in consequence of which the amount and strength of the light affecting that part varies considerably. Long-lived plants, which grow vigorously in height and breadth, alter in their relation to the sun in various stages of growth, and must also alter their form in a corresponding manner, or, at least, must alter the direction and position of their green tissues. All this requires a multiplicity of contrivances which are, as a matter of fact, innumerable, and the exhaustive treatment of which is scarcely possible. In order to obtain a general view, it will be better to pick out some of the most remarkable of the long series of arrangements whose significance lies in this, that each species of plant receives for its green organs neither too much nor too little light, and to describe them in their relations to light as types of smaller or larger groups.

We will begin with those arrangements which are rendered necessary by a peculiar habitat, and, first of all, we will investigate those plants which have taken up their quarters in caves or grottoes, and there pass through all their stages of development. In deep excavations shut off entirely from the light, as well as in those which have been formed without human interference, and those which have been dug in order to obtain metal ore, coal, salt, and water, plants with chlorophyll-bearing cells and tissues are completely wanting. The plants which we find there consist only of pale fungi, which live on the scanty organic compounds which the infiltrating rain-water brings with it into the depths from the surface of the sunny land above, or which have established themselves on organic decaying bodies brought there by chance or intentionally by animals and men. It is otherwise in caves, mines, grottoes, pits, and wells, where light is able to penetrate from above or from the sides, even if only through a comparatively small aperture. Truly the vegetation developed there is not very luxuriant, but it is a very remarkable circumstance that there, as a rule, the plants are still green. What actually astonishes one at first sight of this vegetation, flourishing in caves illuminated only from one side, is the fact that they exhibit the most beautiful and vigorous green, a green much fresher, indeed, and more pronounced than that displayed by the plants outside. Thus the Hart's Tongue (*Scolopendrium officinarum*), widely distributed in Southern Europe, when adorning the deep shady walls of rocky ravines is coloured a much brighter green than when it grows on stony places in the open country where light can reach it from all sides. Also the liver-worts which cover the damp stones with their leaf-like thallus, in grottoes through which waters ripple, show there in the half-light a distinctly richer green than when outside the grotto. But this phenomenon is most striking in the prothallia of some ferns belonging to the section of the Hymenophyllaceæ, and in many mosses.

A tiny moss, called popularly the Luminous Moss, but which has received from

botanists the name *Schistostega oemundacea*, has even attained a certain celebrity on this account. It is found distributed throughout the Central European granite and slate mountains, but is only to be met with in clefts of the rocks, caves and similar spots. As a rule it covers the yellow, clayey earth and the decayed and disintegrated pieces of stone which form the soil of these caverns and small grottoes. On looking into the interior of the cave, the background appears quite dark, and an ill-defined twilight only appears to fall from the centre on to the side walls; but on the level floor of the cave innumerable golden-green points of light sparkle and gleam, so that it might be imagined that small emeralds had been scattered over the ground. If we reach curiously into the depth of the grotto to snatch a specimen of the shining objects, and examine the prize in our hand under a bright light, we can scarcely believe our eyes, for there is nothing else but dull lustreless earth and damp, mouldering bits of stone of a yellowish-grey colour. Only on looking closer will it be noticed that the soil and stones are studded and spun over in parts with dull green dots and delicate threads, and that, moreover, there appears a delicate filigree of tiny moss-plants rising star-like, pale bluish-green in colour, and resembling a small arched feather stuck in the ground. This phenomenon, that an object should only shine in dark rocky clefts, and immediately lose its brilliance when it is brought into the bright daylight, is so surprising that one can easily understand how the legends have arisen of fantastic gnomes, and cave-inhabiting goblins who allow the covetous sons of earth to gaze on the gold and precious stones, but prepare the bitter disappointment for the seeker of the enchanted treasure; that, when he empties out the treasure which he has hastily raked together in the cave, he sees roll out of the sacks, not glittering jewels, but only common earth.

It has been mentioned that on the floor of rocky caves one may discern by careful examination two kinds of insignificant-looking plant-structures, one a web of threads studded with small crumbling bodies, and the other bluish-green moss-plants resembling tiny feathers. The threads form the so-called protonema, and the green moss-plants grow up as a second generation from this protonema. How this comes about will be described in another place; here it only interests us that the gleams do not issue from the green moss-plants, but only from their protonema. If this is viewed under the microscope a sight is presented like that depicted in fig. p on Plate I. From the much-branched threads, composed of tubular cells, which spread horizontally over the ground, numerous twigs rise up vertically, bearing groups of spherical cells arranged like bunches of grapes. All the cells of a group lie in one plane, and each of these planes is at right angles to the rays of light entering through the aperture of the rocky cleft. The grape-like groups of cells have longer or shorter stalks, but they always appear in rows side by side and behind one another, placed cup-like, that the anterior groups do not deprive those behind them of too much of the light which enters the cavity. Each of the spherical cells contains chlorophyll-granules, but in small number; usually four, six, eight, or ten and they are always collected together on those sides of the

cells which are turned towards the dark background of the cave. There they are grouped like a mosaic, and usually so that one green granule forms the centre, while the others surround it very regularly in a circle. Such groups remind one of the arrangement of the floral-leaves in Forget-me-not flowers, and give a very ornamental appearance to the cells. Taken together, these chlorophyll-granules form a layer, which, under a low power of the microscope, appears as a round green spot. With the exception of these chlorophyll-granules the contents of the cell are colourless and transparent, and share these characteristics with the unusually delicate cell-wall. The light which falls on such cells through the opening of a rocky cleft behaves like the light which reaches a glass globe at the further end of a dark room. The parallel incident rays which arrive at the globe are so refracted that they form a cone of light, and since the hinder surface of the globe is within this cone, a bright disc appears on it. If this disc, on which the refracted rays of light fall, is furnished with a lining, this also will be comparatively strongly-illuminated by the light concentrated on it, and will stand out from the darker surroundings as a bright circular patch. This lining has the power of manufacturing organic substances in the spherical cells of the protonema of the Luminous Moss, and in this way the scanty incident light is turned to the greatest possible advantage; it is refracted and concentrated on those places where the chlorophyll-granules are situated, and consequently these receive in the dark recesses an amount of light which amply suffices for their special functions. It is well worthy of notice that the patch of green chlorophyll-granules on the hinder side of the spherical cell extends exactly so far as it is illumined by the refracted rays, while beyond this region, where there is no illumination, no chlorophyll-granules are to be seen. The refracted rays which fall on the round green spot are, moreover, only partially absorbed; in part they are reflected back as from a concave mirror, and these reflected rays give the cells of the protonema a luminous appearance. This phenomenon, therefore, has the greatest resemblance to the appearance of light which the eyes of cats and other animals display in half-dark places, only illumined from one side, and so does not depend upon a chemical process, an oxidation, as perhaps does the light of the glow-worm or of the mycelium of fungi which grows on decaying wood. Since the reflected light-rays take the same path as the incident rays had taken, it is clear that the gleams of the *Schistostega* can only be seen when the eye is in the line of the incident rays of light. In consequence of the small extent of the aperture through which the light penetrates into the rock cleft, it is not always easy to get a good view of the phenomenon described. If we hold the head close to the opening, we thereby prevent the entrance of the light, and obviously in that case no light can be reflected. It is, therefore, better when looking into the cave to place one's self so that some light at anyrate may reach its depths. Then the spectacle has indeed an indescribable charm. What has just been said about the isolated cells is exemplified in groups of cells placed behind one another, of which usually many thousands are found in a very small area.

Among the mosses which find their home in deep shady places, principally in hollow tree-trunks, and are noticeable there for their glossy green, *Hookeria splendens* is especially worthy of attention. To be sure, its leaves do not shine as brightly as the protonema of *Schistostega*, but the appearance is, on the whole, much the same, and here also a similar development is the cause. The leaves of *Hookeria* are comparatively large, but at the same time very thin and delicate. They are composed of a single layer of rhombic cells, very convex above and below, so that the whole leaf may be compared to some extent to a window with very small so-called "bull's eyes" in the glass. The chlorophyll-granules are here arranged with far less regularity than in the protonema of the Luminous Moss, but they are heaped together just as in that plant on the side of the leaf facing the ground, that is to say, which is turned from the light. The side which is turned in the direction of the scanty incident light has no chlorophyll layer. The hemispherically-convex cells, opposed to this scanty light which falls on one side of the leaf, act like glass lenses; they concentrate the weak light on the chlorophyll-granules heaped up on the other side; but, on the other hand, light is also reflected, and this gives rise to the green lustre with which the *Hookeria* shines forth from its dim surroundings.

Like those plants which inhabit rocks, grottoes, and stone clefts, and the shady obscurity of hollow trunks, plants whose habitat is at the bottom of the sea, and in the depths of lakes and ponds, are only visited by weakened sunbeams. The illumination becomes the dimmer the deeper the habitat in question lies below the surface of the water, since the intensity of the light penetrating the water diminishes with the increasing length of the distance travelled. At a depth of 200 metres under the sea complete darkness reigns; at 170 metres the intensity of illumination is like that observed above the water on a moonlight night; such an illumination is insufficient to enable chlorophyll-bearing plants to manufacture organic substances from the absorbed raw materials, even although the plants were provided with all possible aids for the collection of this exceedingly weak light. It is only at a depth of not more than 90 metres that light is sufficient for the chlorophyll cells to decompose carbonic acid, and this depth is ascertained to be the lowest limit of chlorophyll-bearing plants. Moreover, these figures are only applicable in the most favourable circumstances in broad daylight, and only when the water is very clear and transparent, which really only seldom occurs, we might even say exceptionally. The substratum on which the submerged plants are situated, whether sand, mud, or rock, is usually sloping, and is most visited by the oblique rays of the sun. Frequently also small solid particles are suspended in the water, even in water which in the aggregate appears to be quite clear, and so the light is again considerably weakened. This happens especially in the neighbourhood of steep coasts, where the seething of the waves works uninterruptedly at the destruction of the solid shore, and consequently at a depth of 60 metres on such steep declivities, plants possessing chlorophyll are seldom met with.

Generally speaking, the vegetation in the sea is limited to a zone of about 30 metres

in depth, whose width varies with the steepness of the shore. Below this narrow girdle, vegetation is practically extinguished, and the depths of the ocean are in all parts of the globe a plantless waste. This statement is not contradicted by the fact that sea-wracks have been found showing a length of 100, it is alleged even of 200 and 300 metres, as, for example, the celebrated *Macrocystis pyrifera*, between New Zealand and Tierra del Fuego. These sea-wracks do not rise perpendicularly from the bottom to the surface of the sea, but proceed from steep declivities, and grow at an angle to the surface, on which account they often take the direction of the current. One must imagine their position in the water to be almost like that of the Floating Pondweed, or the Water Crowfoot (*Potamogeton fluitans* and *Ranunculus fluitans*), which occur in brooks only a few decimetres deep, and nevertheless may attain a length of more than a metre.

It is naturally to be expected that plants which grow in the dim light, deep under the water on a rocky reef, would behave exactly like the grotto-inhabiting Luminous Moss; and if the barrel-shaped and spherical cell-structures connected into chains, the cyst-like and berry-shaped outgrowths of the unicellular Caulerpas and Halimedas, as well as the faceted cell-walls of those diatoms living in the abysses of the sea in dim twilight, are accepted as contrivances by which light is collected and focussed on those places within the cells where the chlorophyll-bodies are heaped up, then no mistake will be made. Several of the sea-inhabiting Florideæ and sea-wracks belonging to the genera *Phylocladia*, *Polysiphonia*, *Wrangelia*, and *Cystosira*, even exhibit under the water a peculiar luminosity which may be compared with that of the Luminous Moss, although the optical apparatus is here essentially different. In the superficial cells of the luminous Phylocladias are to be found plates segregated out of the protoplasm and closely adhering to the outer walls, which contain a large number of small crowded lenticular bodies. From these minute lenses the blue and green rays are chiefly reflected, and thus the peculiar iridescence is produced. But, on the other hand, yellow and red rays are refracted on to the chlorophyll-granules, and consequently these plates must be regarded as an apparatus for focussing the light, which, by its passage through the thick layers of water, has undergone a considerable diminution.

In the depths of the sea, however, another optical phenomenon must be taken account of, by which the illumination of chlorophyll-granules in the plants growing there becomes in the end a favourable one, and that is the fluorescence of erythro-phyll, the fluorescence of that red pigment to which the Florideæ owe their characteristic colour. In order to make this phenomenon clear, it seems necessary first of all, to rectify a wide-spread error with regard to the colour of water generally, and particularly of sea-water. In the very attractively-written work by Schleiden, *The Plant and its Life*, the seventh chapter, which treats of the sea and its inhabitants, begins with the following lines:—"O learn to know them, the horrible deeps, which are concealed beneath the shining treacherous surface. You descend, the blue of the sky vanishes, the light of day is gone, a fiery yellow surrounds you, then a flaming red, as if you were plunged into a watery sea-hell, without

glow and without warmth. The red becomes darker, purple, finally black, and impenetrable night holds you enthralled". This description is founded doubtless on the account of divers of the olden time, according to which red light should predominate in the abysses of the ocean. These accounts must, however, be retained only to the following extent. The cliffs and the rocky bottom to which the divers descended might have been richly carpeted with red Florideæ, possibly also just then the strata of water above were filled with those unicellular red algæ, which cause the so-called "flowers of the sea". In the neighbourhood of the mouth of the Tejo at times a superficial area of sixty million of square metres is coloured scarlet by *Protococcus Atlanticus*, a unicellular alga, 40,000 of which cover only a square millimetre; and *Trichodesmium Erythraeum*, another microscopic alga consisting of bundles of delicate articulated threads in innumerable milliards, fills the watery strata in the Red Sea as well as in the Indian and Pacific Oceans, so that there immeasurable stretches of water receive a dingy red colouring. When these algæ make their appearance the sea is said to blossom, and at those times the depths may appear to the diver as shrouded in a reddish-yellow twilight. At times the same colour has even been observed in the Lake of Geneva when its waters had been disturbed; it is due to the fact that the blue rays of the incident light are weakened by the fine atoms suspended in the water. With respect to this occurrence, we may consider that the above-mentioned accounts of divers are not the results of intentional deception, but only refer to particular cases. They cannot be applied universally. As a matter of fact, the colour of sea-water, in direct as well as in reflected light, is blue, and the diver who carries on his work at the bottom of the untroubled and non-blossoming sea, is not surrounded there by red, but by blue light. The greater the quantity of salt contained in the water, the deeper the blue. This blue nowhere appears so beautiful and so deep in tint as in the Dead Sea, and in the region of the Gulf Stream and of the Kurosiur, where the water is particularly rich in dissolved salts, and also has in the upper strata a comparatively high temperature. The blue colour of the water is explained thus: from among the rays which are characterized by different wave-lengths and different refrangibility (which, taken together, form colourless daylight, and which we admire separated in the colours of the rainbow), the red, orange, and yellow are absorbed in their passage through the water, and only those rays which are characterized by high refrangibility, viz. the blue, are allowed to pass through. The rays on the further side of the red, not perceptible to our eyes, the so-called dark heat-rays, are likewise absorbed in their passage through the water, and an object at some depth under water would therefore only be reached by rays of high refrangibility, particularly blue rays. The conditions of illumination for plants growing in the depths of the ocean are consequently in reality quite unfavourable. It is not only that a portion of the light falling on the surface of the water is reflected, and the other portion is weakened by its passage through the water, but besides, those rays which are necessary to the formation of organic matter by the chlorophyll-granules in the

plant cells are abstracted from the light which passes through; for the chlorophyll-granules need just the red, yellow, and orange rays if they are to perform their functions; only under the influence of these rays can the decomposition of carbonic acid, the separation of oxygen, and the formation of carbohydrates, take place. The blue rays do not assist at all in this respect; they are even hurtful to these processes, since they assist the oxidation, that is, the decomposition of organic substance. Consequently, phycoërythrin, the red pigment of the Florideæ, now appears, and indeed so abundantly, that the chlorophyll-granules in the interior are quite hidden by it. This colouring-matter displays a very marked fluorescence, that is to say, it absorbs a large portion of the light rays falling on it, and gives out other rays of greater wave-length. The blue rays are to some extent changed by it to yellow, orange, and red, and thus the chlorophyll-granules finally receive those rays which act as the propelling force in the decomposition of carbonic acid. But this also affords an explanation of the remarkable phenomenon that sea-plants are only coloured green close to the shore, and only in the most superficial layers of water, while lower down they appear red. Only quite on the surface the emerald-like *Ulvaceæ* and *Enteromorphas* sway hither and thither, forming thus a light-green belt; these algæ are to be sought for in vain in the depths beneath; of the plants which flourish below this region it can no longer be said that they grow green; this mark of vegetation has entirely vanished. Green has given place to red. All the innumerable Florideæ are reddened—sometimes a delicate carmine, sometimes a deep purple; then again a light brownish-red and a dull, dark crimson, and as we admire in the bush the innumerable gradations of green colour, so is the eye delighted in the manifold shades of red, in which the different variegated species of Florideæ, intermixing with one another, display themselves.

Let us now leave the blue twilight of the sea-depths, and set foot on the strand lapped by the blue waves sparkling with white foam, and climb up one of the rocky crags rising there above the seething waters. Around us is the bright daylight, and broad terraces of rock thickly overgrown with plants, all brilliantly illuminated by the unclouded sun. But where is that fresh green which we expect to find up here according to the foregoing definitions in herbs and bushes? Here are not green, but grey foliage and branches, white-haired stems and leaves, and the whole woven and bound together into a carpet, which looks as if it had been strewn with ashes, or as if the wind had for a week brought hither the dust from the neighbouring streets and deposited it. The plants here on the sunny rocks have provided themselves with silky, woolly, and felted coverings for the purpose of softening the too glaring light. In the depths of the sea and in the grottoes of the slate rocks, the light was too weak; here, however, it is too strong. The chlorophyll-granules tolerate neither the one nor the other; they require light of a definite intensity. If the limit, which in this matter is exactly defined for each species, is overstepped, the chlorophyll is destroyed. Too much light may be no less injurious to the plants than if the chlorophyll-granules are condemned to inactivity on account of the want of light.

How quickly a glaring light is able to destroy the chlorophyll can be well seen in the green Sea-lettuce on the shore below. In a high sea a violent wave tears fragments of the Ulvaceæ, known under the name of Sea-lettuce, from the coast-rocks; a second wave as it rushes up washes the leaf-like structures on to the shingle of the shore, and there it remains with other débris lying amongst the stones. The sea now becomes calm, the sky has cleared, the sun's rays are again burning with undiminished strength on the shadeless strand. As long as the Sea-lettuce adhered closely to the rocks below the surface of the water it displayed a brilliant emerald green; the water in which it was submerged to some little depth, even at a low tide, sufficed to somewhat temper the sunlight; but the stranded *Ulva* is deprived of this light-regulating covering of water, and in a few hours its chlorophyll is destroyed. It is turned yellow, and looks like a lettuce-leaf which has lain for a week in a dark cellar. A similar appearance is also seen in confervas and spirogyras which fill stagnant pools of water with their masses of united filaments. Two decimetres below the water they display a beautiful dark-green colour, while close to the surface they appear a yellowish-green, and if the pool dries up so that the masses of filament come to lie on the damp slime, in two days they are quite bleached; the undimmed sunlight has completely destroyed the chlorophyll in the cells. In the depth of beech-groves the Woodruff (*Asperula odorata*) raises its leaves arranged in whorls on the stem; over it the thickly-leaved branches of the beeches bend together, forming a roof through whose interstices only here and there a weak sunbeam finds its way into the depths. In the dim light the leaf-stars of the Woodruff appear of a deep, dark-green tint. Now the axe of the woodcutter resounds through the forest—the beeches are felled, the shading roof of foliage is demolished, and the floor of the wood is exposed to the glaring sunbeams. Within two weeks the Woodruff can no longer be recognized; it has become sickly and pale; the leaf-stars have lost their dark green, and the chlorophyll has been destroyed by the glaring light. The same thing occurs with ferns as with the Woodruff. In the dimness of the floor of the forest, between steep-walled rocks, and on shady northern declivities they are tinted dark green; in sunny situations they become pale, and then are noticeably retarded in growth. All these plants are not organized to adapt themselves, in the case of an alteration of the illumination of their habitat, to the new conditions and to protect themselves from the undimmed rays falling on them. They are only fitted for the shady floor of the wood, and an over-abundance of light is their death.

But how is the vegetation protected in a habitat where during the whole of the vegetative period full light predominates, where the sun makes itself felt from rise to setting with uninterrupted power? It has already been pointed out that the plants on the broad ridges and terraces of the rocky shores of the Mediterranean are shrouded in dull grey, clothed in silk or wool, or else overstrewn with chaff-like scales, and consequently have lost their fresh green colour. In reality it is not quite correct to say that they have "lost" the green, for their parenchymatous cells, especially those of the palisade and spongy tissues in the foliage-leaves, are no less

rich in chlorophyll-granules than those of shaded plants, only they have developed from their epidermal cells those structures which have been previously described as covering hairs. These cellular structures, devoid of chlorophyll, cover over the green tissue, and thus give to the leaf in question a grey or white colour. They play the part of awnings and light-extinguishers, and when they are removed the leaf appears just as green as one that has been plucked from the shade of the wood.

Silky, velvety, and woolly coats may thus doubtless take on the function of extinguishers. We meet, therefore, the same contrivances apparently which already on a previous occasion have been treated of, viz. when describing the protective measures against excessive transpiration. Thus through these structures two birds are killed with one stone. All contrivances which keep off too glaring sunbeams, and thereby hinder the destruction of chlorophyll, at the same time diminish transpiration; and inasmuch as these contrivances perform two such important functions for the life of plants, their wide distribution and great diversity is accounted for. Suited to the conditions, adapted to the habitat and season of the year, and in harmony with other developments, they change in a thousand ways, and thus display a diversity which can scarcely be treated exhaustively. Besides the covering hairs which are placed above the green tissue, as a protection and shade against too intense light, and at the same time against excessive transpiration, obviously all the other contrivances previously described are to be taken into account. The development of one or several layers of cells, filled with watery cell-sap, above the tissue exposed to the sun's rays, the thickening of the cuticular layers, the waxy and varnish-like coatings, the lime incrustations and salt excretions, the diminution of the illuminated portion of the leaf-surface, the formation of wrinkles, folds, pits, and grooves on the illumined surface of the foliage—all these are able to interrupt and diminish the rays and to reduce their intensity to the right degree.

The number of the special contrivances which simply secure chlorophyll from destruction by too glaring light, without at the same time protecting the green tissue from excessive transpiration, must indeed be very small. First of all, we may mention the dry thin-skinned scales which in many plants are inserted between the green leaves. These are seen, for example, in species of the genus *Paronychia*, which in masses have their habitat in sunny places, and produce silver-glittering transparent scales, devoid of chlorophyll, close to that portion of the stem from which the small green leaves originate. These scales, which are designated stipules, and which, here, are usually as large, occasionally even larger, than the green leaves, take up naturally such a position in the plants growing on shadeless hillocks that the sun's rays first of all fall on them, and only reach the green leaflets in a weakened state.

Another arrangement, which indeed is able to restrict the destruction of the chlorophyll by the sun's rays, without affecting transpiration, consists in the development of a blue or violet colouring-matter in those cells which compose the superficial covering of the leaves and stem which is directly illuminated by the sun's

rays. Such an arrangement is found, for example, in the leaves of the aromatic *Satureja hortensis*, originally growing wild in the Mediterranean floral district, and cultivated in gardens under the name of Summer Savory, of which leaves a small portion is represented in cross section on Plate I., fig. q, printed in colours. Before the sunbeam reaches the chlorophyll-granules of the green cells in the middle of the leaf, it must pass through these epidermal cells filled with violet sap, and here it becomes so weakened and also so changed that an injurious influence on the chlorophyll-granules is out of the question. We must not omit to notice here that the violet light-reducing colouring-matter in the epidermal cells is more abundantly developed the intenser the light to which the plants in question are exposed. If plants of the Summer Savory grow in shady places, their leaves remain green on the upper sides, and scarcely any traces of the violet colouring-matter are to be discovered in the epidermal cells. If, on the other hand, they have germinated in shadeless districts, both stem and leaves are coloured dark violet, and the cell-sap in the epidermal cells is then of that deep tint shown in Plate I., fig. q. Some years ago I cultivated seeds of the Summer Savory in my experimental garden at a height of 2195 metres above the sea-level in the Tyrol. As is known, the sun's rays are much more powerful in the Alpine heights than in the valley, and it was therefore, indeed, to be expected that the leaves of the germinating plants would be of a much darker tint than in the shadeless gardens of the valley below. In fact, the colouring-matter developed in extraordinary abundance; even the stems and leaves actually became a dark brownish violet. It is, therefore, beyond question that the quantity of colouring-matter in the epidermal cells directly exposed to the sun increases with the increase of the intensity of the light. Obviously this protection of the chlorophyll can only occur when the plants possess the materials for forming the pink colouring-matter in their green organs. When this is not possible, when the characteristic constitution of the protoplasm does not permit the development of the colouring-matter named in the foliage-leaves, the chlorophyll must be protected against the glaring light in another way, and if the plant species is not able to ward off the over-abundance of sunlight in the new position, it perishes entirely. Flax (*Linum usitatissimum*) was sown next to the Sumner Savory in the Alpine experimental garden—a plant which bears the direct sunlight quite well, and flourishes in the valley as well as in the plains in sunny situations. However, the light of the Alpine region was too brilliant for the germinating flax-plants; the leaves turned yellow, their chlorophyll was destroyed, and the seedlings became pale and perished. Flax has not the capacity of manufacturing the colouring-matter in its superficial cells, and it is also not organized to produce covering hairs on the leaves and stem, or to thicken its cuticular strata suitably—in a word, to adapt itself to the position and to provide itself, under the increased light intensity, with corresponding sun-shades and light-extinguishers. While close at hand, the Summer Savory, which requires just as much warmth, and an equally long vegetative period as flax, reached the flowering stage, and even produced ripe fruits capable of germinating, the flax died before the development of its flowers.

From these culture experiments two things may be learned: first, that a very brilliant light is able to influence the distribution of plants and to set up an impassable barrier for many of them; and secondly, that many plants have the capacity of adapting themselves to various degrees of light intensity; but in consequence of this they occasionally develop such a varying character that they might be mistaken for wholly different species. But I shall return again later when speaking of the origin of new species to this result of cultivation. Here we shall only discuss, in order to prove and make clear the connection between certain plant characteristics and the conditions of illumination, how it happens that the surface of foliage exposed to the direct rays of the sun is so frequently coloured violet or red, or is completely covered over with hairs, while the leaves of the same species if they have been developed on shady soil in dispersed light are coloured green, and remain almost bare; how it happens that plants of one and the same species in the deep valleys possess but few hairs, or are provided with but thin cuticular layers, but on the sunny slopes of high mountains are shrouded in thick grey or white fur, or appear thick and almost leathery in consequence of strongly-developed cuticular layers. In order to prevent misconception, it must indeed be pointed out here that all this only refers to the epidermis over the green tissue which is exposed to direct or diffuse sunlight, chiefly, therefore, to the *upper* side of the foliage-leaf, and that when the blue colouring-matter and also the covering hairs are developed on the under side of the leaf, or in floral leaves devoid of chlorophyll, they have then an essentially different significance, which will be described in the next section.

When describing the protective measures of the green tissues against the dangers of over-transpiration, the vertical direction of branches, flattened shoots, phyllodes, and especially of the green leaf-surfaces, was pointed out. The leaves of irises, and of the so-called compass-plants, the flattened outspread petioles, with their edge directed towards the zenith, in so many Australian trees and shrubs, were there more especially described, and finally it was pointed out that the leaflets of many papilionaceous plants, and the leaves of numerous grasses, temporarily take up a position by sinking, rising, and folding together, in which not the broad side, but the narrow edge, is exposed to the vertical rays of the mid-day sun.

A leaf-surface which assumes one of these positions with regard to the sun will transpire much less than a foliage-leaf on whose broad surface the mid-day sun falls vertically, or almost vertically; but by such a position the leaf is also afforded a protection against the too vivid light of noon. The rays which reach a vertical leaf-surface at morning and evening are not so intense as to be able to destroy chlorophyll; they have rather just that intensity which the chlorophyll-granules require for their activity. Therefore, by this arrangement the function of the chlorophyll-granules is not restricted, but is actually assisted, and in this sense the vertical direction of the green surfaces is to be looked upon also as an arrangement for regulating the activity of the chlorophyll-granules.

It is evident after this explanation that herbs with vertically-directed leaf-

surfaces are never to be met with in shady places. On the floor of a thick wood grow no irises and no compass-plants; these are at home on the ridges of rocky mountains, and on treeless prairies, and if it happens that a seed of such a plant falls into the shade of a wood and germinates there, developing foliage-leaves, then the leaf-surfaces do not assume a vertical position, and twist and bend themselves until their broad surface is turned towards the scantily-penetrating diffuse light. If the light falls from above through the interstices of the leafy covering, the leaf-surface becomes horizontal and parallel to the ground; if the crests of the trees close together to form a thick, opaque canopy, and the diffuse light penetrates from the side between the trunks of the trees, the leaf-laminae bend and turn to the openings of the wood, giving the impression that they are looking out longingly to the sunny country which borders the dense, deep-shaded forest.

The same thing is seen under every small shady bush, and, generally speaking, in all places where dissimilar tall plants overlap one another, and where the leaves of the lower are arched over by those of the higher plants. If they belong to different species, they cannot be said to have any consideration for one another. Each looks out only for itself, and the lofty species do not trouble themselves about the inferior stuff which arises from the soil under their leaves. If in the depths below there are plants which find all they require in the diffuse light and the green rays passing through the leafy roof, very well; if not, these lower plants must perish in the shade. But it is otherwise if the leaves overlapping each other belong to one and the same branch, to one and the same plant; where they must co-operate for the weal of the whole plant, and the whole can only maintain itself in the struggle for existence by harmonious division of labour. Therefore care must be taken that no leaf shall take too much light away from another; that one shall protect and support the other; that neighbours shall not jostle if one or the other has to bend, turn, and extend itself in order to best adapt itself to the incident light.

And this foresight actually occurs. It is exhibited, first of all, in the position of the leaves on the stem, or in other words, in the regulation of the intervals between the places of origin of neighbouring leaves; secondly, by the fact that the stalks of the green leaf-blades have the capacity of rising and sinking, twisting and bending, and also of elongating if required; and thirdly, through the form which the leaf-surfaces possess.

---

## 2. THE GREEN LEAVES.

Distribution of the green leaves on the stem.—Relation between position and form of green leaves.  
—Arrangements for retaining the position taken up.—Protective arrangements of green leaves against the attacks of animals.

### DISTRIBUTION OF THE GREEN LEAVES ON THE STEM.

Landscape painters tell us how difficult it is to treat foliage correctly, and at the same time artistically; how hard, for instance, so to reproduce the leafy crown of maples, beeches, elms, limes, and oaks that they shall immediately be recognized for that which they are intended to represent, and at the same time that that effect and tone shall be produced which is aimed at in the picture. The variety of the foliage is caused not least by the distribution of the green leaves on the branches, and by the branching dependent upon this; things as definite as possible for each species of tree, and, generally speaking, for every plant.

On cutting various leafy branches and observing the distribution of the leaves on them, the following differences first strike the eye. In numerous plants it is seen that two or more leaves originate at the same height on a branch, while in many other plants, at a particular level of the stem or branch, only a single leaf is produced. In order to be able to understand these circumstances, it is advisable to imagine the leaf-bearing shoot or stem as a cone. The apex of the cone corresponds to the upper end, and the base of the cone to the lower portion, i.e. to the oldest part of the shoot. The whole shoot is not at any time in a completed state; it continues to grow at the apex, and at the upper part is not only younger, but is also less bulky than the older portions lying nearer to the base. It can, therefore, indeed be quite well compared to a cone, although this form is only seldom so noticeably to be met with as in the following diagrammatic figures.

That which applies to the age of the various portions of the shoot naturally applies also to the leaves projecting from the shoot. That is to say, the lower leaves of the shoot are the older, the upper leaves are the younger. On looking at the top of the cone (see fig. 98), the places of insertion of the older leaves appear to arise, first of all, from the circular disc which forms the base of the cone, while the younger leaves originate close to the apex, therefore close to the centre. The stem is to a certain extent divided up by the leaves into sections one above another. Usually it is somewhat thickened or knotted at those places where the leaves project from it, and therefore the places of origin of the leaves are designated as *nodes*. Each portion of the stem lying between two successive nodes is called an *internode*. When two leaves project at the same height from the stem, they are inserted opposite one another, not unlike the two extended arms of a human body, and they appear on the cone-shaped stem (whose cross section at all heights forms a circle) at a distance from one another of exactly half the circumference of the circle ( $180^\circ$ ), (fig. 98<sup>1</sup>). If three leaves spring together from the stem,

as, for example, in the Oleander, these are separated from one another in a horizontal direction by one-third of the circumference of the circle ( $120^\circ$ ). Several leaves springing from the same height form together a *whorl*, and the distance of the individual members of a whorl from one another is called the horizontal distance, or the *divergence*. The divergence amounts to  $\frac{1}{2}$  in fig. 98<sup>1</sup>, and  $\frac{1}{3}$  in fig. 98<sup>2</sup>, of the circumference of the circle, and can be thus shortly expressed by means of these fractions.

It is very remarkable that the whorls which follow after and above one another according to their age on one and the same shoot do not originate at corresponding places of the circumference, but are displaced regularly with regard to one another. Thus the point of origin of the second two-membered whorl in

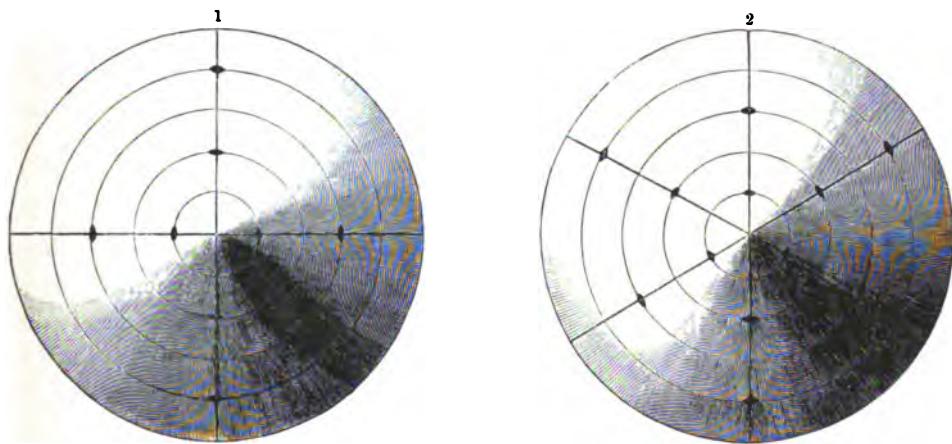


Fig. 98.—Plan of Whorled Phyllotaxis.

<sup>1</sup> Two-membered Whorl. <sup>2</sup> Three-membered Whorl.

fig. 98<sup>1</sup> is shifted through a quarter of the circumference (i.e. through  $90^\circ$ , a right angle) from the point of origin of the first, oldest, and lowest two-membered whorl. The third whorl is again shifted through a right angle with regard to the second, and so it continues up the stem as far, generally speaking, as foliage-leaves are to be found on it. If the stem is elongated in the case described, four rectilineal lines (*orthostichies*) appear to be developed on it (fig. 98<sup>1</sup>). If a whorl is composed of three leaves, and if the successive whorls be displaced through one-sixth of the circumference, as, for example, in the Oleander (see fig. 98<sup>2</sup>), six rectilineal series of leaves or orthostichies originate, running parallel to one another down the stem.

The leafy stem can also be imagined as divided into stories, each of which displays the same number, position, and distribution of the leaves, and agrees completely in the plan of its construction with the adjoining story. In one such case (fig. 98<sup>1</sup>), each story possesses four leaves in the form of a cross; in another case (fig. 98<sup>2</sup>), it possesses two sets of three leaves separated from one another by a distance of  $60^\circ$ . If the stories standing above one another are separated, they would be so alike in arrangement as to be easily mistaken for one another. Each

originates below and ends above exactly like the one over and the one under it, and the only difference rests in the fact that the sections closer to the summit of the branch have smaller diameters, and often also a somewhat different outline of their members. The plan of construction is, however, as stated, exactly the same in the successive stories.

In those instances where each story consists of two whorls of leaves, which are displaced with regard to one another through a certain angle, especially in the very common case where the whorl is two-membered, i.e. where the leaves are opposite one another in pairs, and where the successive pairs of leaves are alternately displaced through a right angle from one another, appearing thus like a cross, the leaves are said to be *decussate*. This arrangement is seen especially in maples and ashes, in lilac and olive-trees, in elder and honeysuckle, in labiates, gentians, Apocynaceæ, and numerous other families of plants.

Still more common than this arrangement of the leaves is that which has been called the *spiral*. Here at one and the same height only a single leaf originates from the stem, and therefore all the leaves of a stem are not only shifted with respect to one another in a horizontal, but also in a vertical direction. If one imagines the nodes of a stem with decussate leaves to be so arranged longitudinally that the leaves are inserted no longer at the same heights, but at definite intervals above one another, then from the decussating, i.e. whorled, arrangement a spiral is produced. In many willows (*e.g. Salix purpurea*), and very regularly also in some buckthorns (*e.g. Rhamnus cathartica*), in the speedwells (*e.g. Veronica spicata* and *longifolia*), and also in many composites leaves arranged partly in whorls and partly in spirals occur on the same axis, and doubtless the one merges into the other, but for the sake of clearness it is better to keep them distinct, and to draw a line between them, even though it be an imaginary one.

It may be observed that stems with spirally-arranged leaves are constructed exactly like those which bear leaf-whorls, and that they consist of many stories each displaying a similar plan of construction, so that the number, position, and distribution of the leaves is repeated in each story, and as a matter of fact the following plans of construction are actually to be found very frequently.

*First case.* In each story only two leaves arise from the circumference of the stem. These two leaves are displaced with regard to one another in a horizontal as well as vertical direction, and their horizontal divergence amounts to half the circumference of the circle ( $180^\circ$ ) as shown in the plan in fig. 99<sup>1</sup>. If a continuous line be drawn from the point of insertion of each lower older leaf to the younger one next above it on the surface of the stem, this will display the form of a spiral. It has been called the *genetic spiral*. In the first case here discussed it forms in each story only a single spiral band. This arrangement is repeated in the second, third, and perhaps in many other stories which follow successively on the same axis. In this way the lower leaf of the second, third, or fourth story always lies exactly above the lower leaf of the first story. The same applies to the upper leaves of all the stories. Thus two rectilineal lines or orthostichies are formed on

the circumference of the stem by the leaves situated vertically above one another. The two lines are opposite, or, what comes to the same thing, they are separated from one another by half the circumference of the stem. This arrangement of the leaves, which may be observed, for example, on the branches of elms (*Ulmus*) and limes (*Tilia*), is called the one-half phyllotaxis.

*Second case.* Three leaves are developed in one story, each at a definite height, an under, a middle, and an upper leaf. In a horizontal direction two of the leaves following one another in age are always shifted from one another through a third part of the circumference (see fig. 99<sup>2</sup>). If the point of insertion of the lower leaf is connected with that of the middle leaf, and this again with that of the upper leaf by a line, and this line is continued to the beginning of the next story, a single spiral is thus formed surrounding the stem. Now above the story just described, which we will call the lowest, a second follows, which is again provided with three leaves arranged in exactly the same way. The lower leaf of the second story is situated vertically above the lower leaf of the first story, the middle above the middle, and the upper above the upper leaf, and the same arrangement is continued through all the stories. In this manner three rectilineal lines, or orthostichies, arise on the circumference of the stem from the leaves situated above one another, and each of the lines is separated from the other two by  $\frac{1}{3}$  of the circumference. This arrangement, which is to be found on the upright branches of alders, hazels, and beeches, is called the one-third phyllotaxis.

*Third case.* Five leaves originate in each story, which are designated according to age as the first, second, third, fourth, and fifth, the lowest being the oldest, the highest the youngest. These five leaves give place to one another in a horizontal direction, and the shifting, *i.e.* the horizontal distance between two leaves next in age, amounts to  $\frac{2}{5}$  of the circumference of the circle (see the plan, fig. 99<sup>3</sup>). If the five leaves are joined together in succession according to their age, a spiral line is obtained consisting of two revolutions, and the "genetic spiral" consequently forms two circuits round the stem. If a stem, whose leaves are arranged in this manner, is built up of two or several stories, then the similarly numbered leaves are situated in straight lines above one another, the first (lowest) leaves of all the stories form together one straight line (orthostichy); in the same way the second, the third, &c. Thus five lines are developed on the circumference of the stem by the leaves situated one above the other, and each line is separated from another by  $\frac{2}{5}$  of the circumference. This arrangement, which is found in oaks, round-leaved willows, and in many buckthorns, is designated the two-fifths phyllotaxis.

*Fourth case.* Eight leaves are to be found in each story, which may again be numbered from one to eight according to their age. Any two successive leaves are separated from one another horizontally by  $\frac{3}{8}$  of the circumference (see fig. 99<sup>4</sup>). If a line be drawn starting from the first and lowest leaf, joining all the eight leaves of the story in the order of their ages, this forms a spiral line, or "genetic spiral", which traverses the stem three times. In a stem consisting of several such stories, the leaves named by the same numbers are placed in straight lines above one

another, and accordingly eight rectilineal lines (orthostichies) run down the stem. Each line is separated from its neighbour by  $\frac{1}{8}$  of the circumference. This arrangement, which occurs in roses, raspberries, pears, and poplars, in laburnums, and in the barberry, is called the three-eighths phyllotaxis.

Yet a *fifth case* is very often to be found in trees and bushes with narrow leaves, viz. in the Almond-tree, in the Goat's-thorn, in the Sweet Willow, in the Sea Buckthorn, and many Spiraea bushes. Each story contains thirteen leaves.

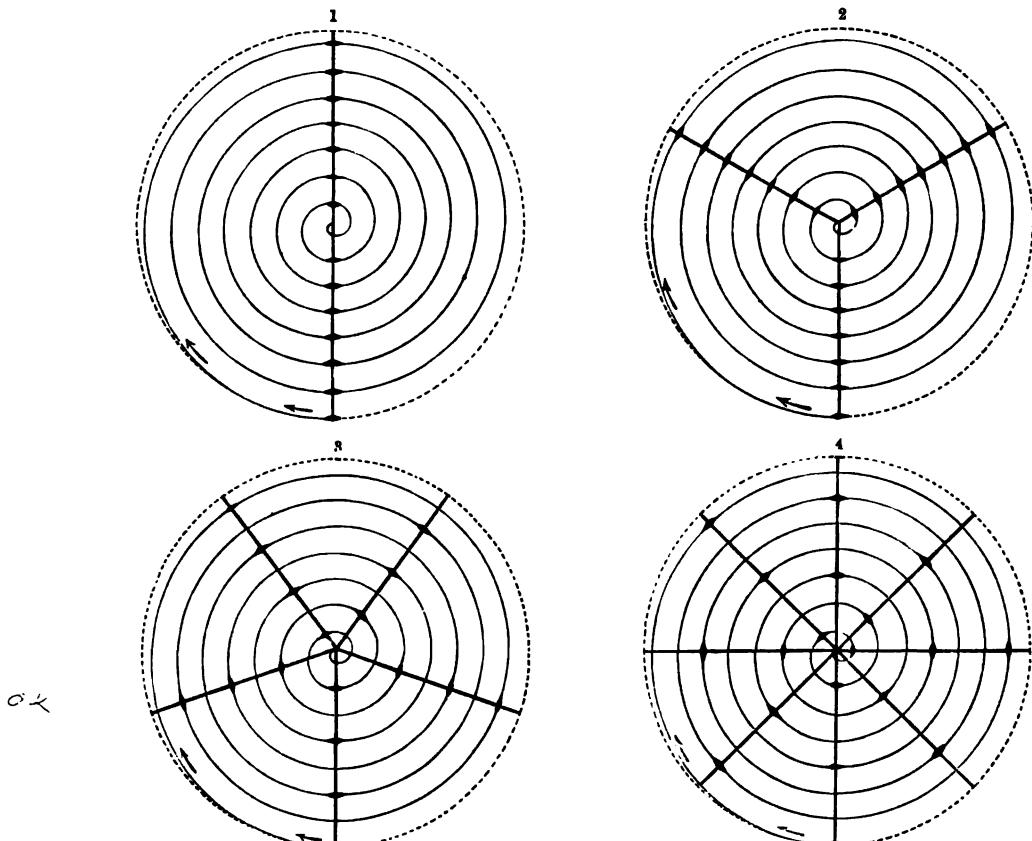
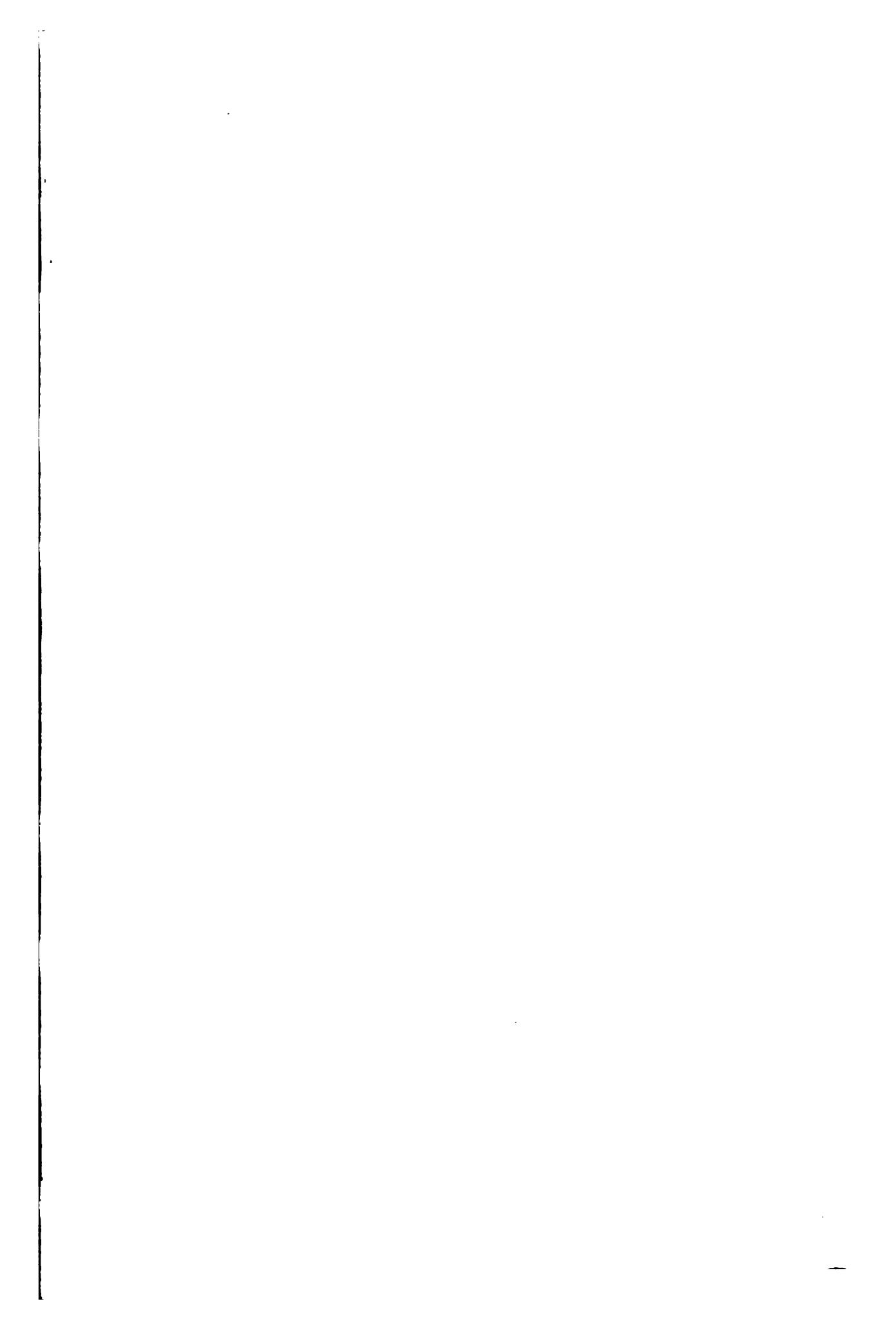


Fig. 99.—Plan for Spiral Phyllotaxis.

<sup>1</sup> One-half Phyllotaxis. <sup>2</sup> One-third Phyllotaxis. <sup>3</sup> Two-fifths Phyllotaxis. <sup>4</sup> Three-eighths Phyllotaxis. The conical stem horizontally projected; the points of insertion of the leaves on the circumference of the stem marked by a dot.

which may be connected by a spiral line, *i.e.* a "genetic spiral", with five revolutions. The number of the straight lines here amounts to thirteen, and the distance between two leaves following one another in age is  $\frac{1}{13}$  of the circumference, *i.e.*  $138^\circ$  (see fig. 100).

Not so common, or rather not demonstrable with the same precision, are instances in which one story shows twenty-one leaves which are connected by a genetic spiral with eight revolutions; and where a story includes thirty-four leaves which are connected by a genetic spiral with thirteen revolutions. In the one case any two leaves next one another in age in a story are separated from one









3 2044 102 802 014

